

# Rhodora

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### TAXONOMY OF *NERISYRENIA* (CRUCIFERAE)<sup>1</sup>

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A small genus of perennial mustards, *Nerisyrenia* is limited, for the most part, to the Chihuahuan Desert. The widest ranging taxon, *N. camporum*, extends into the southern and western edge of the Edwards Plateau and the southern fringe of the Rio Grande Plains of Texas. The remaining species show regional or highly localized distributions, correlated, in the majority of cases, with the occurrence of gypsum ( $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ ).

Rollins (1939) studied the genus and treated the three species known to him. Subsequently, two additional species were described (Johnston, 1941; Rollins, 1941b); since that time *Nerisyrenia* has remained unexplored systematically. Therefore, a monograph of the group was undertaken. In addition to field observations and morphological studies, extensive cytological and flavonoid chemical studies were completed on all species. The latter approaches were extremely informative and essential in establishing species limits and relationships. Therefore, this systematic treatment is an amalgam of the total evidence gathered during the study.

#### TAXONOMIC HISTORY

Events leading to the establishment of *Nerisyrenia* began in 1850 with Asa Gray's description of *Greggia camporum*. He chose the generic name to honor the then recently deceased Dr. Josiah Gregg, even though he was aware that the name, *Greggia*, had been previously applied by Engelmann to the rosaceous genus *Cowania*. Apparently Gray was not aware that the name *Greggia* had been used, even earlier, by Gaertner. In any event, Gray's appellation was rejected.

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<sup>1</sup>This paper is based on a dissertation completed in the Department of Botany, The University of Texas, Austin, Texas, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.



Greene (1895) attempted to rectify the nomenclatural problem of *Greggia*, now containing an additional species, *G. linearifolia* Watson, by offering the name *Parrasia* for the genus. This name, however, proved equally unsuitable as Greene discovered "soon after the appearance of the third volume of the *Index Kewensis*" that the name *Parrasia* had been previously applied by Rafinesque (Greene, 1900). Greene then proposed the presently accepted name *Nerisyrenia* for the two known species.

The genus remained with two species until the late 1930's and early 1940's. During that period, and as a result of I. M. Johnston's trips into northern Mexico, three species were added to the genus, *Nerisyrenia incana* Rollins, *N. castillonii* Rollins and *N. gracilis* I. M. Johnston.

The above mentioned species constituted the genus when this investigation was initiated. Recent field work in northern Mexico by Drs. M. C. Johnston, B. L. Turner, and their colleagues and students, including myself, has revealed several new taxa referable to *Nerisyrenia*. In this treatment the genus comprises nine species and one variety.

#### CYTOLOGY

Prior to this study, chromosome numbers had been reported for only two species of *Nerisyrenia*. Rollins (1939) reported a gametic number of  $n = 7$  for *N. camporum*, based on a collection from Brewster County, Texas. Subsequently, Rollins (1966) reported two additional counts for the same species:  $n = 9$  from material also collected in Brewster County, Texas, and  $n = 11$  based on material from Coahuila, Mexico. Material of *N. linearifolia*, from Culberson County, Texas, was also reported for the first time as  $n = 9$ .

As indicated in Table I, I have obtained counts for the remaining species of the genus. I have also obtained additional counts for the two previously reported taxa. Counts reported here were gathered from over 200 individuals from throughout the range of each species, and it is felt that the survey is a fair portrayal of chromosomal patterns within the genus. In addition, several populations of one species of the closely related genus *Synthlipsis*, *S. greggii* A. Gray, were examined for chromosome numbers (Table I). Complete voucher citations are available from the author on request.



### Materials and Methods

In the field, bud material was collected and put into a modified Carnoy's solution (chloroform : 95% ethanol : glacial acetic acid, 4:3:1, v/v). In the laboratory, the fixed buds were stored under refrigeration until examined. Chromosome numbers were determined from pollen mother cells obtained from suitable anthers squashed in aceto-carmin stain (Smith, 1947). Voucher specimens for all counts are on deposit in The University of Texas Herbarium (TEX).

In most instances, bud material was collected from three to five individual plants per population in order to detect intrapopulation variation, if present. However, this was not possible when buds were scarce in a given population; consequently, several populations are represented by counts for only a single individual.

### Results and Discussion

As indicated in Table I, 221 chromosome counts representing 112 populations of the nine species of *Nerisyrenia* were made in the course of this study. The genus as a whole exhibits a rather wide array of chromosome numbers, with diploid, polyploid, aneuploid and, apparently, dysploid numbers represented. With few exceptions, aneuploidy is found in all species. To facilitate the discussion that follows, the species are considered individually.

***Nerisyrenia camporum*.** This taxon consists of two major cytological races (Table I), diploids ( $2n = 18$ ) and tetraploids ( $2n = 36$ ). From presently available data, the diploids appear to be limited to the Chihuahuan Desert of north-central Mexico, entering into the United States in southern Brewster and Presidio Counties, Texas. The tetraploids appear to be distributed peripherally to the diploids. Morphological differences could not be found to distinguish the two cytotypes with their similar variations and forms. Diploid and tetraploid plants were never encountered in the same population; however, populations of one cytotype were collected within a few airline miles of the other. Aneuploidy occurs within both cytotypes. For example, near Lajitas, in southern Brewster County, Texas, predominantly diploid populations are found. However, three plants collected in the area yielded counts of  $2n = 21$  (*Bacon 1056b*),  $2n = 22$  (*Bacon 1054d*) and  $2n = 27$  (*Powell 2191*). The triploid plant usually exhibited two or three trivalents per cell in addition to a few bivalents and several univalents.



Table I. Summary of Chromosome Numbers for *Nerisyrenia* and *Synthlipsis*

<i>Taxon</i>	$2n =$	<i>Locality (number of populations examined/total plants counted)</i>
<i>N. camporum</i>	18	MÉXICO: Coahuila (13/22), Durango (1/5). TEXAS: Brewster Co. (4/7), Presidio Co. (6/9).
	19+	MÉXICO: Coahuila (0/1). TEXAS: Presidio Co. (0/1).
	21+	TEXAS: Presidio Co. (0/1).
	22+	TEXAS: Brewster Co. (0/1).
	27	TEXAS: Presidio Co. (1/1).
	32	MÉXICO: Chihuahua (2/4).
	34+	TEXAS: Reeves Co. (0/1).
	36	MÉXICO: Chihuahua (1/4), Coahuila (5/7). NEW MEXICO: Otero Co. (1/1). TEXAS: Brewster Co. (6/8), Culberson Co. (1/2), Hudspeth Co. (4/6), Jeff Davis Co. (1/1), Loving Co. (1/1), Pecos Co. (1/1), Presidio Co. (2/4), Reeves Co. (3/4), Ward Co. (1/2).
	38*	TEXAS: Culberson Co. (1/1).
	40	TEXAS: Hudspeth Co. (2/3).
	41+	MÉXICO: Coahuila (0/1).
	Ca. 44+	MÉXICO: Coahuila (0/1).
	58*	TEXAS: Culberson Co. (0/1).
	<i>N. linearifolia</i> var. <i>linearifolia</i>	18
19		NEW MEXICO: Otero Co. (2/2).
20+		NEW MEXICO: Otero Co. (0/1).
34+		TEXAS: Reeves Co. (0/1).
36		TEXAS: Reeves Co. (3/8), Ward Co. (1/3).
<i>N. linearifolia</i> var. <i>mexicana</i>	36	MÉXICO: Nuevo León (1/2).
<i>N. gypsophila</i>	18	MÉXICO: Chihuahua (2/4).
<i>N. gracilis</i>	18	MÉXICO: Nuevo León (1/1).
	34	MÉXICO: Nuevo León (3/6).
	36	MÉXICO: Nuevo León (2/2), San Luis Potosí (5/6).
	38	MÉXICO: Nuevo León (1/1).
<i>N. powellii</i>	38	MÉXICO: Coahuila (1/1).
<i>N. johnstonii</i>	20	MÉXICO: Coahuila (1/1).
<i>N. castillonii</i>	20	MÉXICO: Coahuila (1/2).
	40	MÉXICO: Coahuila (11/21).



Table I — continued

	48	MÉXICO: Coahuila (1/1).
	58	MÉXICO: Coahuila (2/5).
	59+	MÉXICO: Coahuila (0/1).
<i>N. turneri</i>	20	MÉXICO: Nuevo León (2/3).
	32	MÉXICO: San Luis Potosí (5/10).
	33+	MÉXICO: San Luis Potosí (0/1).
	36	MÉXICO: San Luis Potosí (1/1).
	Ca. 38+	MÉXICO: San Luis Potosí (0/1).
<i>N. incana</i>	20	MÉXICO: Coahuila (9/12).
	21	MÉXICO: Coahuila (1/1).
	23	MÉXICO: Coahuila (1/1).
<i>S. greggii</i>	20	MÉXICO: Chihuahua (1/1), Coahuila (8/10), San Luis Potosí (2/3).

+Aneuploid plant in euploid population.

\*Plants from same population.

The temptation to recognize the triploid plant as a hybrid between the diploid and tetraploid is great. However, I have found tetraploid populations no closer than 10 airline miles to the east and 25–30 airline miles to the west of the Lajitas site; nevertheless, their presence in the area cannot be ruled out. The triploid might also have arisen from the union of a diploid, unreduced gamete and a reduced diploid gamete. Subsequent outcrossing with diploid plants in the population could then lead to at least a few aneuploid derivatives, as found in this area.

A similar situation was encountered near Torreon, Coahuila. Three plants from this population (*Bacon & Hartman 1344*) were determined as  $2n = \text{ca. } 36$ ,  $41$  and  $\text{ca. } 44$ . Approximately three airline miles to the east, diploid populations have been documented. The plant with  $2n = \text{ca. } 44$  is suggestive of pentaploidy, possibly derived from an unreduced tetraploid gamete and a reduced diploid gamete. Again, outcrossing to tetraploid neighbors could yield plants with  $2n = 41$ .

Additional aneuploid plants were encountered sporadically in both diploid and tetraploid populations. Two plants with  $2n = 19$  were found in otherwise diploid populations, one west of Cuatro Ciénegas, Coahuila (*Bacon & Leverich 1188b*) and one from Presidio County, Texas (*Bacon & Hartman 1423b*). One plant from Reeves County, Texas (*Bacon 1059c*), exhibited a chromosome



complement of  $2n = 34$ . Two populations, separated by about 50 airline miles, were collected in Hudspeth County, Texas, and contained plants with  $2n = 40$ ; one population had two plants with this number (*Bacon 947c,d*) plus a tetraploid individual; the other population (*Bacon 945*) returned chromosomal data from only a single plant. In Culberson County, Texas, two additional chromosomal variants,  $2n = 38$  and  $2n = 58$ , were encountered, both in the same population. With the exception of the  $2n = 58$  plant, *all* the above mentioned aneuploids formed the maximum number of bivalents at first meiotic metaphase; the  $2n = 58$  plant exhibited univalents, trivalents and quadrivalents at first metaphase.

Evidence for a possible third regional cytotype within *Nerisyrenia camporum* has been found near Aldama, Chihuahua. Three plants from one population (*Bacon & Hartman 1346*) were clearly  $2n = 32$ . A further count, provided by Dr. A. M. Powell, from material about 20 miles east of the former population was  $n = \text{ca. } 16$ . Population samples from this region are few, however, and future investigations will undoubtedly show other types to be present.

In spite of several collection trips to the area from which Rollins (1939) obtained the count of  $n = 7$  for *Nerisyrenia camporum*, I have been unable to corroborate his report.

***Nerisyrenia incana*.** This taxon gave rather consistent counts of  $2n = 20$  (Table I). However, three plants yielded aneuploid numbers of  $2n = 21$  (two plants) and 23. Additionally, the count of  $n = 11$  reported by Rollins (1966) for *N. camporum* should be referred to this taxon; examination of his voucher specimen (*Rollins & Tryon 58293*, GH!) revealed the plant to have siliques typical of *N. incana*.

***Nerisyrenia gypsophila*.** This species has proven to be consistently diploid with  $2n = 18$  (Table I). However, the taxon has been sampled only from the type locality and surrounding area; consequently, further sampling should be undertaken before this number is accepted as characteristic.

***Nerisyrenia linearifolia* var. *linearifolia*.** This taxon consists of two cytological races (Table I), diploids ( $2n = 18$ ) and tetraploids ( $2n = 36$ ); occasional aneuploid plants also occur. Three plants from the White Sands area of New Mexico yielded aneuploid counts; two had  $2n = 19$ , and one had  $2n = 20$  (*Bacon 1046c*). In contrast to two additional plants from the same population with  $2n = 36$ ,



a single plant from Reeves County, Texas, was determined as  $2n = 34$  (*Bacon 1060c*).

**Nerisyrenia linearifolia** var. **mexicana**. This taxon is known, at present, from only two counts, both  $2n = 36$  (Table I).

**Nerisyrenia powellii**. This species is known chromosomally from only a single count of  $2n = 38$  (Table I). The count came from a "mass bud collection" taken in a population where buds were scarce; therefore, this number should not be taken as characteristic until further sampling can be accomplished.

The chromosome number of this taxon is clearly polyploid and suggestive of amphiploidy via hybridization between some  $x = 9$  taxon and an  $x = 10$  taxon. However, since those species with  $x = 10$  have a distinctive chemistry (with the exception of *N. incana*) as compared to those species with  $x = 9$ , one might expect the flavonoid chemistry of this taxon to reflect such an origin through an "additive flavonoid profile". The chemical evidence did not support this suggestion. Considering the widespread occurrence of aneuploidy within the genus, this number probably represents aneuploid variation from the tetraploid number of  $2n = 36$ .

**Nerisyrenia gracilis**. This species yielded counts of  $2n = 18, 34, 36$  and  $38$ , with  $2n = 36$  as the predominant number (Table I). One plant with  $2n = 34$  (*Bacon 1013b*) provided the only instance other than univalent-multivalent oddities, of meiotic irregularity seen during this study. Lagging chromosomes were seen in some pollen mother cells at first metaphase; micronuclei were present at late second telophase in a number of cells. Other plants with  $2n = 34$  had normal meiosis. This taxon proved difficult to count, and many of the determinations reflect only a single plant per locality; therefore, populational chromosome numbers may prove more complex than indicated.

**Nerisyrenia johnstonii**. A single count of  $2n = 20$  (Table I) has been obtained for this rare, extremely localized endemic.

This species and *Nerisyrenia incana* are thought to represent the most "primitive" species in the genus (see PHYLOGENY). The occurrence in both species of the diploid number of  $2n = 20$  suggests  $x = 10$  as the original basic number for the genus.

**Nerisyrenia castillonii**. This taxon exhibited chromosome numbers of  $2n = 20, 40, 48, 58$  and  $59$ , with the typical number of  $2n = 40$  (Table I).



The diploid counts of  $2n = 20$  came from two rather depauperate plants, perhaps in their first year of growth.

Those plants with  $2n = 58$  were collected during the initial stages of this investigation. After chromosome number determinations, I felt that these collections probably represented amphiploid derivatives of *Nerisyrenia castillonii* and some other taxon in the area. Subsequent attempts, on three different occasions, to re-collect this material from the same locality and surrounding area met with failure. As more chromosome counts were accumulated and the variation in number became apparent, I changed my attitude as to the amphiploid nature of these collections, and thus I include them in this taxon. I was not able to determine the metaphase configurations in these plants, but all countable cells at second division clearly showed 29 chromosomes.

**Nerisyrenia turneri.** This species yielded counts of  $2n = 20, 32, 33, 36,$  and ca. 38, with  $2n = 32$  predominating (Table I). The counts of  $2n = 33$  and 38 came from a population in which three other plants were determined as  $2n = 32$  (*Bacon & Hartman 1330*). The count of  $2n = 36$  was derived from a single plant (*Bacon & Hartman 1329*), the only material yielding a count from that population.

Counts of  $2n = 20$  were derived from two populations. Morphologically, these two populations were somewhat atypical for the species in that they had narrower leaves and more slender siliques than most populations encountered; however, their flavonoid profiles were identical to the bulk of this taxon. Perhaps they represent populations more similar morphologically to ancestral populations of *Nerisyrenia turneri*.

Although the typical chromosome number of this species,  $2n = 32$ , is unusual for the genus and suggests a base number of  $x = 8$ , it seems clear that this number has been derived from an original base of  $x = 10$ . This taxon is most closely related to *Nerisyrenia castillonii*, which has the basic number of  $x = 10$ . These two species share a similar flavonoid chemistry with *N. johnstonii* (see FLAVONOID CHEMISTRY) which also has a chromosome number of  $2n = 20$ . These relationships plus the two populations of this taxon with  $2n = 20$  suggest that the typical number in this species,  $2n = 32$ , has been derived through polyploid drop (Grant, 1971,



p. 224) from  $2n = 40$ . Perhaps the aneuploid counts for this taxon represent “remnants” of the process by which this new number was attained.

**Synthlipsis greggii.** This taxon exhibited consistently diploid numbers of  $2n = 20$  (Table I), confirming the single previous report for this species (Rollins & Rüdénberg, 1969).

The reference to the diploid-polyploid populations noted in some species of *Nerisyrenia* as cytotypes or cytological races reflects the absence of external morphological features differentiating between the ploidy levels. This lack of morphological differentiation suggests that the polyploid populations may be autoploid in origin. The inclusion of diploids and their autopolyploid derivatives within a single species is biologically warranted (Lewis, 1967; Mosquin, 1967). However, as has been shown in some plant groups, most notably in *Gilia* (Day, 1965; Grant, 1964, 1971; see Grant 1964, 1971 for review of other groups), strong reproductive barriers can exist between individuals which are almost indistinguishable morphologically; therefore, in such groups, what is treated as a single taxonomic species consists, in fact, of two or more biological species, termed sibling species (Grant, 1964, 1971). In plants, sibling species are often associated with allopolyploidy (Grant, 1971, p. 30). The inclusion of two biological species within a single taxonomic species, although often the most pragmatic solution for routine identifications, is misleading and obscures the biological relationships within the concerned group (Grant, 1964, 1971). Possibly, sibling species exist within some species of *Nerisyrenia*. The identification and recognition of sibling species, however, requires taxogenetic analysis, and such data were not gathered during this study. Therefore, I have recognized as species those populations with similar morphology, regardless of ploidy level, while noting their chromosomal distinctiveness with the term cytotype. Hopefully, this taxonomic recognition coincides with the biological integrity of the recognized species.

Chromosomal data have been useful in many instances in supporting species delimitation. However, such data have been most helpful in delimiting phyletic groupings. Clearly, two “chromosomal lines” exist, one based on  $x = 10$  and the other based on  $x = 9$ . This dichotomy is further supported by the flavonoid chemistry



of the various species (see FLAVONOID CHEMISTRY). *Nerisyrenia incana* is anomalous within the genus in possessing a chromosomal base of  $x = 10$  while exhibiting a flavonoid chemistry typical of those species based on  $x = 9$ ; this taxon is thought to be a "primitive" species, the ancestors of which gave rise to the  $x = 9$  line.

In those instances of aneuploidy seen in this study, the extra chromosomes are felt to be chromosomes of the "somic" type as opposed to supernumerary or accessory chromosomes; none of the features usually associated with accessory chromosomes, *e.g.*, heterochromaticity or smaller size (Brown, 1972; Swanson, 1958), was observed; also, the general lack of trivalent or multivalent formation on the part of the "extra" chromosomes and their expression as univalents or bivalents is in keeping with the results of numerous reports concerning somic aneuploids, both induced (Rick & Notani, 1961; Dhillon & Garber, 1960; Vasek, 1956) and naturally occurring (W. Lewis, 1962; Lewis, Suda & McBryde, 1967; Lewis, Oliver & Suda, 1967; H. Lewis, 1951, 1953). Indeed, my own observations of meiotic cells in this study suggest the same. In some plants which had consistent bivalent formation at metaphase I, an occasional meiocyte at second prophase was seen to have unequal distribution of chromosomes, which suggests that nondisjunction occurs with at least some frequency throughout the genus.

These observations, plus the fact that *Nerisyrenia linearifolia*, *N. gracilis*, *N. turneri*, *N. powellii* and *N. castillonii*, are strongly rhizomatous, may help explain the array of numbers in these taxa. The remaining taxa, *N. camporum*, *N. incana* and *N. gypsophila*, are tap-rooted. It is perhaps significant that the chromosomal variation within *N. incana* and *N. gypsophila* is either not known (to date) or sporadic and near the diploid level. Within *N. camporum*, if one ignores possible intrapopulational hybridization among cytotypes, the variation in chromosome number is, again, sporadic, and except in one instance, near the euploid level, either diploid or tetraploid.

One must also bear in mind that the presence of agamospermy (Grant, 1971) cannot be eliminated; my attempts to observe embryo sac formation have proved fruitless. Also, the possibility of polyploid complexes (Grant, 1971), especially in *Nerisyrenia castillonii*, must be kept in mind. The resolution of these possibilities must await further chromosome sampling on a more massive level and experimental hybridization among cytotypes.



Table II. Summary of Populations of *Nerisyrenia* and *Synthlipsis* Examined Chromatographically for Flavonoids

<i>Taxon</i>	<i>Locality (number populations examined/total plants examined)</i>
<i>N. camporum</i>	MÉXICO: Chihuahua (3/7), Coahuila (21/34), Durango (1/3). TEXAS: Brewster Co. (13/23), Culberson Co. (2/6), El Paso Co. (1/4), Hudspeth Co. (4/12), Jeff Davis Co. (1/1), Loving Co. (1/1), Presidio Co. (9/20), Reeves Co. (2/4), Ward Co. (2/5).
<i>N. linearifolia</i> var. <i>linearifolia</i>	MÉXICO: Coahuila (3/3). NEW MEXICO: Chaves Co. (1/1), Eddy Co. (1/3), Otero Co. (2/2), Socorro Co. (1/4). TEXAS: Culberson Co. (2/7), Reeves Co. (3/13), Ward Co. (3/6).
<i>N. linearifolia</i> var. <i>mexicana</i>	MÉXICO: Coahuila (1/1), Nuevo León (5/7).
<i>N. gypsophila</i>	MÉXICO: Chihuahua (2/6).
<i>N. incana</i>	MÉXICO: Coahuila (11/25).
<i>N. johnstonii</i>	MÉXICO: Coahuila (1/2).
<i>N. powellii</i>	MÉXICO: Coahuila (3/8).
<i>N. gracilis</i>	MÉXICO: Nuevo León (11/16), San Luis Potosí (4/8).
<i>N. castillonii</i>	MÉXICO: Coahuila (12/29).
<i>N. turneri</i>	MÉXICO: San Luis Potosí (12/36).
<i>S. greggii</i>	MÉXICO: Chihuahua (1/4), Coahuila (8/15), San Luis Potosí (3/7).

## FLAVONOID CHEMISTRY

The utilization of flavonoid chemistry to gain insight into biological relationships within and among plant taxa is becoming a standard systematic approach. Studies of this nature have been used to discern relationships within hybrid swarms (Alston & Turner, 1963; Turner & Alston, 1959), to support taxonomic discrimination (Bierner, 1973; Cruden, 1972; Crawford, 1973; Gardner, 1974) and to suggest or support phyletic relationships within taxonomic groups (Stebbins *et al.*, 1963; Torres & Levin, 1964; Smith



& Levin, 1963; Mabry *et al.*, 1975). In the hope of obtaining insight concerning the relationships of *Nerisyrenia*, a chemical investigation was initiated.

Populations of all taxa of *Nerisyrenia* and one species of the closely related genus *Synthlipsis* were surveyed for their flavonoid components. Populations from throughout the distributional range of each taxon (Table II), representative of the range of morphological variation of each, were examined. Voucher specimens for all populations studied are deposited in The University of Texas Herbarium (TEX). Complete voucher citations are available from the author on request.

#### METHODS

Chromatographic profiles were established for each collection by extracting a small amount of leaf material overnight with 85% aqueous methanol. The resulting extract was spotted directly on Whatman 3 MM (46 × 57 cm) chromatographic paper. The papers were then developed descendingly in two dimensions; the first, for the long axis of the paper, consisted of tertiary butanol, glacial acetic acid and distilled water (3:1:1; v/v), TBA; the second consisted of glacial acetic acid and distilled water (15:85; v/v), HOAc. The chromatograms were air-dried after each run. To visualize the flavonoid components, the developed chromatograms were viewed over ultraviolet (UV) light (366 nm) in both the presence and absence of ammonia; the color of each spot was noted as was any ammonia induced change in color (Table III).

Isolation of flavonoids for structural analysis was accomplished by a combination of paper and column chromatography (see Bacon & Mabry, 1976 for brief summary of technique). Ultraviolet absorption spectra (Table III) were recorded for each compound isolated, using standard procedures (Mabry, Markham & Thomas, 1970), as well as nuclear magnetic resonance spectra for those compounds isolated in sufficient quantity.

All compounds isolated were glycosides; therefore, each was subjected to acid and enzyme hydrolysis for sugar determination. Sugars were identified by gas-liquid chromatography of their trimethylsilyl ether derivatives (Sweeney *et al.*, 1963; Mabry *et al.*, 1970).



## RESULTS AND DISCUSSION

*Nerisyrenia* elaborates 40 flavonoids of which 31 were isolated and, for the most part, fully characterized. All compounds isolated have been oxygen linked glycosides of the flavonols kaempferol, isorhamnetin and quercetin (Table III). Their distribution among the species is shown in Table IV. A discussion of the significance of the flavonoid pattern within *Nerisyrenia* requires a short digression concerning some aspects of sugars and flavonol glycosides.

The known flavonol glycosides number about 250 (Harborne & Williams, 1975). The most common positions of glycosidic substitution in flavonols are positions 3 and 7 (Figure 1), but flavonols glycosylated in positions 5, 6, 8, 2', 3' and 4' are known (Harborne & Williams, 1975). Sugars may be attached to the flavonol skeleton as single moieties at one position, monoglycosides, as single moieties at two positions or as a disaccharide at one position, diglycosides, and so on through the more highly glycosylated flavonoids.

In disaccharides, two like sugars or two different sugars may be involved. Variations in disaccharides can involve interglycosidic linkages, anomeric forms and ring sizes. Interglycosidic linkages may be between C-1 of one sugar and C-6 of the other, C-1 and C-2, C-1 and C-3 or C-1 and C-4 (see Figure 1). Often, the different linkages are given different names thus identifying the linkage and the sugars involved. For example, the following list indicates the trivial names for the known linkages between disaccharides of  $\beta$ -glucose (Harborne, 1967; Harborne & Williams, 1975; in nature these involve only D-glucose)

- (a) 1  $\rightarrow$  2 linked — sophorose
- (b) 1  $\rightarrow$  6 linked — gentiobiose
- (c) 1  $\rightarrow$  3 linked — laminaribiose
- (d) 1  $\rightarrow$  4 linked — cellobiose.

When L-rhamnose and D-glucose are involved in disaccharide linkages and rhamnose is the terminal sugar, the sugar moiety is termed as follows, the rhamnose carbon listed first:

- (a) 1  $\rightarrow$  6 linked — rutinose
- (b) 1  $\rightarrow$  2 linked — neohesperidose
- (c) 1  $\rightarrow$  3 linked — rungiose.



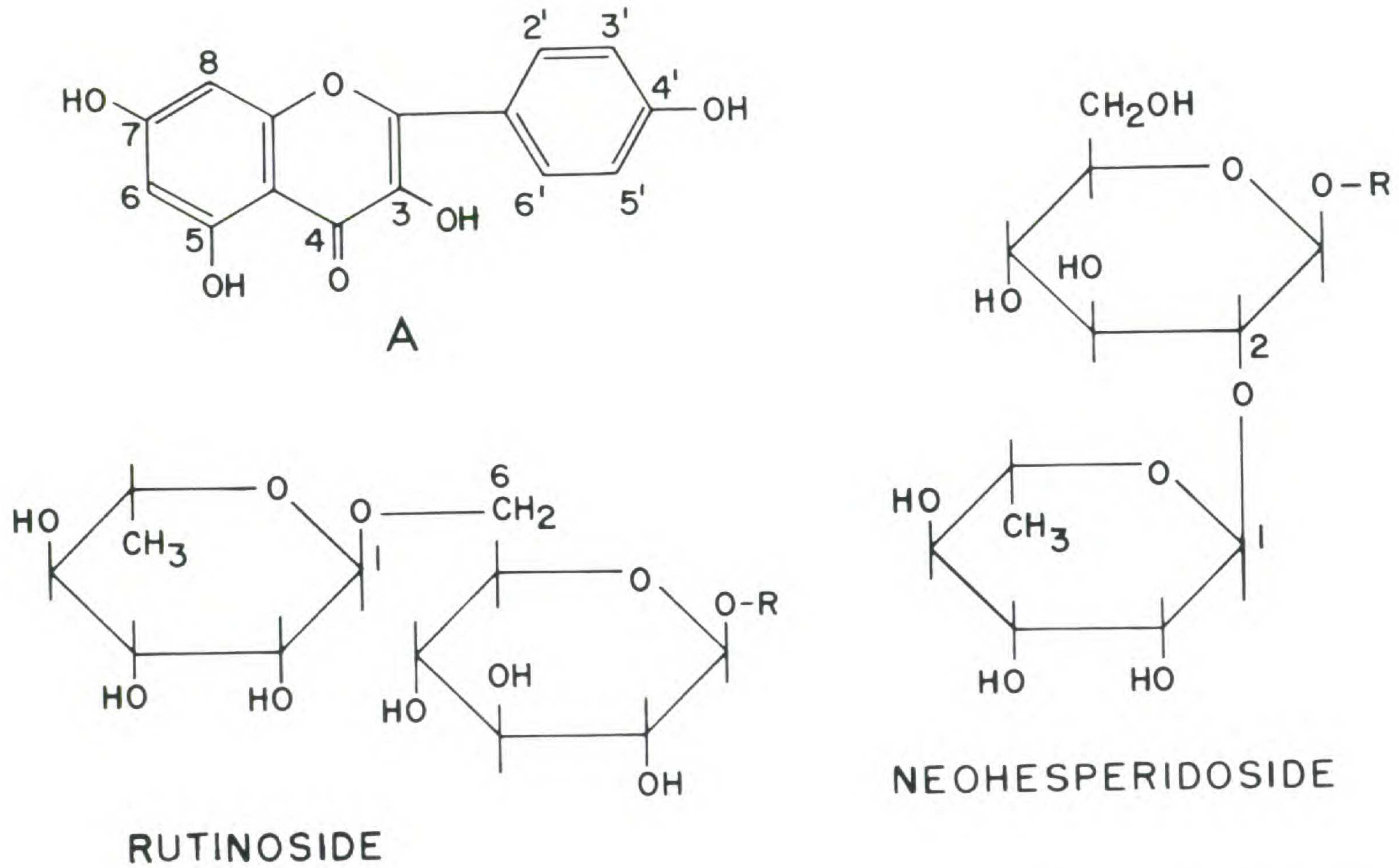


Figure 1. Numbering scheme for flavonoids and representative disaccharides showing different interglycosidic linkages.



While most species of *Nerisyrenia* produce some unique compounds or combinations which suggest species limits (Table IV), the flavonoid data have been most helpful in suggesting species relationships and phyletic groupings.

There is a significant dichotomy within the genus in flavonoid glycosylation patterns. *Nerisyrenia castillonii*, *N. turneri* and *N. johnstonii* all produce diglycosides (disaccharide types) utilizing glucose and/or galactose with the 1 → 2 linkage between the sugar moieties. The remaining species produce diglycosides containing glucose and/or galactose with the 1 → 6 sugar linkage. Furthermore, the neohesperidosides (1 → 2 linked rhamnoglucosides) are absent in the aforementioned species but are present in the remaining species.

Morphologically, *Nerisyrenia incana* is distinctive within the genus, and most closely resembles *N. johnstonii*; the two species share a base chromosome number of  $x = 10$  (see CYTOLOGY). However, these species are very distinctive chemically and fall into opposite glycosylation dichotomies (Table IV). In contrast, *N. camporum*,  $x = 9$ , is almost identical, chemically, with *N. incana*; furthermore, *N. gypsophila*, although producing fewer compounds than either of the above two species, shares with them, with one exception, all the compounds it produces (Table IV).

*Nerisyrenia linearifolia*, *N. gracilis*, and *N. powellii* share several morphological characteristics, such as linear-spathulate leaves with mostly entire margins and a rhizomatous root system, which set these species apart from the species mentioned above. Their chemistry also serves to distinguish these species from the former group (Table IV) and, furthermore, distinguishes *N. linearifolia* from *N. gracilis* and *N. powellii*. Johnston (1941) suggested *N. gracilis* was most closely related to *N. linearifolia* (var. *linearifolia* of this treatment). However, the chemical evidence presented here implies that *N. gracilis* and *N. powellii* are more closely related to each other than either is to *N. linearifolia*.

The distinctive flavonoid chemistry of *Nerisyrenia castillonii*, *N. turneri* and *N. johnstonii* clearly unites these species as a phyletic unit (Table IV); their chromosomal base of  $x = 10$  also separates these species from the bulk of the remaining species (see CYTOLOGY). In addition, their chemistry suggests that they have a phyletic history parallel to, but separate from, the other species within the genus.



Table III.  
Compound Number and Identity, Chromatographic Properties and  
Ultraviolet Absorption Maxima of Nerisyrenia Flavonoids

Compound Number and Identity+	Rf Values		Color Reactions*		Absorption Maxima (nm) <sup>a</sup>					
	TBA	HOAc	UV	+NH <sub>3</sub>	MeOH	NaOMe	AlCl <sub>3</sub>	AlCl <sub>3</sub> +HCl	NaOAc	NaOAc+H <sub>3</sub> BO <sub>3</sub>
1. Acyl Iso-3-glucoside	.51	.23	P	Y	354 265s 253	415 330 270	404	400	386 322 274	359
2. Acyl Iso-3-galactoside	.51	.23	P	Y	354 265s 253	415 330 270	404	400	386 322 274	359
3. K-3-glucoside	.68	.53	P	G	348 300s 266	401 325 275	397	394	368 300 272	354
4. Iso-3-glucoside	.66	.43	P	Y	354 300s 266s 254	414 329 270	398	398	382 320 273	354
5. Q-3-glucoside	.55	.41	P	Y	356 290s 264s 254	406 329 270	436	399	400 326 273	378



Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*				Absorption Maxima (nm) <sup>a</sup>			
	TBA	HOAc	UV	+NH <sub>3</sub>	MeOH	NaOMe	AlCl <sub>3</sub>	AlCl <sub>3</sub> +HCl	NaOAc	NaOAc+H <sub>3</sub> BO <sub>3</sub>
6. K-3-galactoside	.68	.53	P	G	348 300s 266	401 325 275	397	394	368 300 272	354
7. Iso-3-galactoside	.55	.41	P	Y	357 300s 266s 253	416 331 270	407	401	388 322 274	356
8. Q-3-galactoside	.45	.43	P	Y	359 300s 268s 257	410 328 271	436	404	390 328 271	379
9. K-3-sophoroside	.60	.68	P	G	350 300 266	398 326 275	396	396	396 326 275	350
10. Iso-3-sophoroside	.46	.71	P	Y	354 298s 264s 252	410 320 270	407	402	399 322 273	355



Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*		Absorption Maxima (nm) <sup>a</sup>					
	TBA	HOAc	UV	+NH <sub>3</sub>	MeOH	NaOMe	AlCl <sub>3</sub>	AlCl <sub>3</sub> +HCl	NaOAc	NaOAc+H <sub>3</sub> BO <sub>3</sub>
11. Iso-3-digalactoside	.46	.71	P	Y	354 298s 264s 252	410 320 270	407	402	399 322 273	355
12. K-3-neohesperidoside	.70	.79	P	BG	348 298s 265	394 324 274	398	397	380 306 273	350
13. Iso-3-neohesperidoside	.57	.81	P	BY	350 300s 268s 252	406 326 273	403	400	376 318 274	353
14. Q-3-neohesperidoside	.54	.78	P	BY	354 296s 266s 255	401 325 272	436	401	386 322 272	374



Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*				Absorption Maxima (nm) <sup>a</sup>			
	TBA	HOAc	UV	+NH <sub>3</sub>	MeOH	NaOMe	AlCl <sub>3</sub>	AlCl <sub>3</sub> +HCl	NaOAc	NaOAc+H <sub>3</sub> BO <sub>3</sub>
15. Iso-3-gentiobioside	.60	.50	P	Y	353 300s 264s 252	no data	403	394	380 322 270	358
16. Q-3-gentiobioside	.37	.46	P	Y	362 304s 263s 258	414 322 275	438	402	399 326 274	382
17. K-3, 7-diglucoside	—	—	P	YG	—	—	—	—	—	—
18. Iso-3, 7-diglucoside	.21	.76	P	YO	356 270s 257	404 295s 269 252s	403	400	415 265	360
19. Q-3, 7-diglucoside	.20	.62	P	YO	354 266s 256	397 267	434	403	393 265	377



Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*		Absorption Maxima (nm) <sup>a</sup>					
	TBA	HOAc	UV	+NH <sub>3</sub>	MeOH	NaOMe	AlCl <sub>3</sub>	AlCl <sub>3</sub> +HCl	NaOAc	NaOAc+H <sub>3</sub> BO <sub>3</sub>
20. Iso-3-glucoside 7- galactoside	.25	.68	P	YO	356 268s 254	408 300s 268	406	404	421 262	360
21. K-3-glucoside 7- gentiobioside	.12	.78	P	YG	348 320s 268	395 360s 300s 275 248	398	395	397 395s 267	351
22. Iso-3-glucoside 7- gentiobioside	.11	.80	P	YO	356 266s 254	416 291s 263	404	400	416 300s 262	360
23. Q-3-glucoside 7- gentiobioside	.10	.69	P	YO	359 269s 257	398 269	427	401	403 266	379



Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*				Absorption Maxima (nm) <sup>a</sup>			
	TBA	HOAc	UV	+NH <sub>3</sub>	MeOH	NaOMe	AlCl <sub>3</sub>	AlCl <sub>3</sub> +HCl	NaOAc	NaOAc+H <sub>3</sub> BO <sub>3</sub>
24. Iso-3-glucoside 7- glucogalactoside	.09	.81	P	YO	353 264s 253	423 272	406	400	440s 360 263s 253	357
25. Q-3-glucoside 7- glucogalactoside	.06	.72	P	YO	358 266s 255	402 268	441	404	416 263	381
26. K-3-sophoroside 7- glucoside	.22	.75	P	YG	346 263 240	408 365s 300s 274 248	396	396	398 265 260s	350
27. Q-3-neohesperidoside 7-glucoside	.16	.88	P	BY	354 268s 255	399 267	440	404	376 258	375



Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*				Absorption Maxima (nm) <sup>a</sup>			
	TBA	HOAc	UV	+NH <sub>3</sub>	MeOH	NaOMe	AlCl <sub>3</sub>	AlCl <sub>3</sub> +HCl	NaOAc	NaOAc+H <sub>3</sub> BO <sub>3</sub>
28. K-3, 7-digentiobioside	.07	.84	P	YG	350 268	397 292 <sub>s</sub> 266 258	397	395	395 270	350
29. Iso-3, 7-digentiobioside	.06	.78	P	YG	357 262 <sub>s</sub> 254	410 269	408	403	419 262	358
30. K-3-glycoside	.70	.58	P	G	348 262	402 328 272	395	398	372 275	350
31. Iso-3-glycoside	.37	.52	P	Y	356 300 <sub>s</sub> 264 <sub>s</sub> 253	418 330 272	403	400	388 318 271	—
32. Iso-3-glycoside	.27	.70	P	YO	353 300 <sub>s</sub> 267 <sub>s</sub> 254	419 329 272	404	404	—	—



Table III. (Continued)

Compound Number and Identity+	Rf Values		Color Reactions*		MeOH	NaOMe	Absorption Maxima (nm) <sup>a</sup>			
	TBA	HOAc	UV	+NH <sub>3</sub>			AlCl <sub>3</sub>	AlCl <sub>3</sub> +HCl	NaOAc	NaOAc+H <sub>3</sub> BO <sub>3</sub>
33 Unknown	—	—	P	YG						
34 Unknown	—	—	P	YO						
35 Unknown	—	—	P	YO						
36 Unknown	—	—	P	YO						
37 Unknown	—	—	P	BY						
38 Unknown	—	—	P	Y						
39 Unknown	—	—	P	YO						
40 Unknown	—	—	P	YG						

+Iso=Isorhamnetin, Q=Quercetin, K=Kaempferol.

\*P=purple, Y=yellow, G=green, B=brown, O=orange.

<sup>a</sup>only Band I absorption maximum is shown for AlCl<sub>3</sub>, AlCl<sub>3</sub>+HCl, NaOAc+H<sub>3</sub>BO<sub>3</sub>.



Additional support for the phyletic significance of the glycosylation dichotomy within *Nerisyrenia* comes from the flavonoid pattern of *Synthlipsis greggii*. No flavonoids have, as yet, been isolated from this taxon. Nevertheless, the chromatographic profile of this species is very similar to that of *N. turneri* and *N. castillonii*; clearly, this taxon, too, is glycosylating under a 1 → 2 sugar linkage scheme involving glucose and/or galactose. Its chromosomal base is  $x = 10$  (see CYTOLOGY).

#### GENERIC RELATIONSHIPS

Despite some morphological diversity, the taxa composing *Nerisyrenia*, are thought to be more closely related among themselves than any one is to another genus and thus form a natural phyletic unit. Although several genera have been suggested, as direct or indirect relatives of *Nerisyrenia*, I believe only the genus *Synthlipsis* has close affinities.

Although Gray (1850) in his original description of *Nerisyrenia* (as *Greggia*) noted the similarities of *Nerisyrenia* and *Synthlipsis*, subsequent workers such as Bentham and Hooker (1862) and Von Hayek (1911) related *Nerisyrenia* (as *Greggia*) to *Erysimum* and *Syrenia*; indeed, in both the above treatments, *Synthlipsis* and *Nerisyrenia* were placed in different tribes. Bentham and Hooker noted, however, that *Nerisyrenia* had probable affinities with *Synthlipsis*.

In relating *Nerisyrenia* to *Erysimum* and *Syrenia*, Bentham and Hooker emphasized habit, cotyledon position and silique shape; Von Hayek emphasized fruit shape, the presence of branched trichomes, shape of the stigma and characters of the nectaries.

The habit of some species of *Erysimum* is similar to some species of *Nerisyrenia*, but the genera are quite distinct in most respects, as outlined in the following listing:

<b>Erysimum</b>	<b>Nerisyrenia</b>
Fruits strongly compressed or somewhat 4-angled.	Fruits rarely compressed, never 4-angled; usually terete to ob-compressed.
Trichomes usually coarse and T-shaped, sparsely if at all branched.	Trichomes not coarse, dendritically branched.



Cotyledons accumbent to incumbent.	Cotyledons incumbent.
Sepals erect at anthesis.	Sepals spreading to reflexed at anthesis.
Petals yellow to maroon.	Petals white.

I have not made a thorough survey of the nectaries of *Erysimum*, but Snogerup (1967a) has shown that in *Erysimum* sect. *Cheiranthus* the variation in morphology of these glands renders them virtually useless as taxonomic characters.

Chromosomal evidence is also suggestive of the distinctive nature of the two genera. *Erysimum* is multibasic with  $x = 6, 7$  and  $8$  (Snogerup, 1967b); however, several North American taxa have chromosome numbers of  $2n = 36$  (Rollins, 1966, 1970), and Rollins (1966) suggests that these taxa have a base number of  $x = 9$ . Snogerup (1967b) has proposed that the taxa with  $2n = 36$  are hexaploids with a base of  $x = 6$ ; this suggestion is strengthened by the fact that at least one species reported as  $2n = 36$ , *Erysimum pallasii*, has also been reported as  $n = 12$  and  $2n = 24$  (Mulligan, 1966); *Nerisyrenia* is essentially dibasic with  $x = 9$  and  $10$ .

The flavonoid chemistry of *Erysimum*, as is the case for most Cruciferae, has received only cursory attention. However, the scanty data available for *Erysimum* (Maksyutina, Litvinenko & Kovalev, 1966), when compared to the more completely known chemistry of *Nerisyrenia*, suggest the two taxa are distinct; *Erysimum* utilizes different sugar combinations in its accumulated flavonoid glycosides. In short, considering the above, I can see no justification for relating *Nerisyrenia* closely to *Erysimum*.

The relationship of *Syrenia* to *Nerisyrenia* has yet to be fully studied. I have studied only one specimen of the former taxon. Nevertheless, the distribution of the genus in the Mediterranean region of Europe and its morphological differences, including erect, saccate sepals, erect, yellow petals, and mostly tetragonally-shaped fruits (Vasil'chenko, 1939), clearly delineate this taxon from *Nerisyrenia*. While *Syrenia* is unknown chromosomally, the flavonoids of one species have been investigated (Maksyutina, 1967) and are distinct from those of *Nerisyrenia*; *Syrenia siliquosa* accumulates flavonoids glycosylated at the 4'-position, a substitution pattern not found in *Nerisyrenia*, and it also produces disaccharides of glucose and rhamnose in which the glucose moiety is the terminal



Table IV.

Distribution of Flavonoids in *Nerisyrenia*.

Taxon	Compound Number																																												
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40					
<i>camporum</i>			X	X	X							X			X	X	X	X			X	X						X		X			X												
<i>incana</i>			X	X	X							X			X	X		X			X	X						X	X	X			X												
<i>gypsophila</i>			X	X				X				X									X	X								X															
<i>linearifolia</i> var. <i>linearifolia</i>	X	X	X	X	X							X		X		X			X				X					X										X	X	X					
<i>linearifolia</i> var. <i>mexicana</i>			X	X	X							X		X				X	X			X	X				X													X					
<i>powellii</i>			X	X		X	X	X				X	X							X		X		X															X	X					
<i>gracilis</i>			X			X	X	X					X								X		X		X	X															X				
<i>castillonii</i>				X			X		X	X	X																X														X	X	X		
<i>turneri</i>				X			X		X	X	X																X															X	X	X	
<i>johnstonii</i>							X			X	X																															X			



sugar, a reversal of the condition found in *Nerisyrenia*.

By including them in the same subtribe, Schulz (1936) related *Nerisyrenia* to several genera, including *Capsella*, *Heidinia*, *Hornungia*, *Hutchinsia*, *Phlegmatospermum*, *Mancoa*, *Cibotarium* and *Synthlipsis*. Except for the latter three taxa, all the above genera are native to Europe, Asia, the Mediterranean area, or Australia. Although lack of access to research material of these non-American genera has prevented a thorough assessment of their relationship to *Nerisyrenia*, my preliminary study tends to indicate a more remote relationship to *Nerisyrenia* than that shown by the American genera. *Cibotarium*, *Mancoa* and *Synthlipsis* are North American in distribution and are found primarily in the Chihuahuan Desert (Rollins, 1941, 1957, 1959). However, on morphological grounds *Cibotarium* and *Mancoa* are distinct from *Nerisyrenia*. Both the former have much smaller flowers and distinctive fruit shapes as compared to *Nerisyrenia*, although the fruits of both are more or less obcompressed. Furthermore, *Cibotarium* has nearly equal, exerted stamens with purplish anthers (Rollins, 1941a), while *Nerisyrenia* has tetradynamous stamens with yellow anthers. Nevertheless, some species of *Cibotarium* have apically notched fruits as found in two species of *Nerisyrenia*, and further study may prove this genus to be more closely related to *Nerisyrenia*. Information as to chromosome number and chemistry of this group is lacking and reflects its sporadic, highly localized occurrence (Rollins, 1957) and relatively rare collection. Until such information can be obtained and studied, its relationship to *Nerisyrenia* is speculative.

*Mancoa*, through the anomalous species, *M. pubens*, was related by Rollins (1959) to *Synthlipsis* (through its resemblance to *S. elata*). I would agree that *M. pubens* is related to *Synthlipsis* and, therefore, to *Nerisyrenia*. However, in view of the distinctive morphology of *Mancoa*, and in the absence of chromosomal or chemical data for this taxon, speculation as to its direct relationship to *Nerisyrenia* is, at best, tenuous.

In considering the relationship of *Nerisyrenia* and *Synthlipsis*, Rollins (1939) noted the ample technical characters which could be used to distinguish the two genera; these characters included cotyledon position, stigma shape, fruit characters, number of seeds per silique, seed size and presence or absence of dilated petal bases. However, in a later treatment of *Synthlipsis*, Rollins (1959) was less convinced as to the generic distinctness of the two taxa, pri-



marily because of the description of two new species of *Synthlipsis* which was not compatible with some of the previously enumerated differences. For instance, *S. elata* proved to have numerous small seeds with incumbent cotyledons, a state more like *Nerisyrenia* than *Synthlipsis*. Nonetheless, he maintained the taxa at the generic level, noting that merger of the two probably would not be fully warranted even with further study.

I fully concur with Rollins in maintaining the two taxa at the generic level. Even though some characters "overlap" between the two, such as cotyledon position, sepal and petal shape and position at anthesis, and trichome characters, there are many characters which are more or less limited to one or the other of the taxa, and in combination display clear distinction between the two genera. These differences are listed below:

<b>Nerisyrenia</b>	<b>Synthlipsis</b>
Perennials.	Annuals (perennials in <i>S. densiflora</i> ).
Fruit margins never carinate.	Fruit margins carinate.
Fruit apex usually entire, notched only in <i>N. incana</i> and <i>N. johnstonii</i> .	Fruit apex notched.
Fruits obcompressed or terete.	Fruits obcompressed.
Stigma deltoid-sagittate, rarely cylindrical.	Stigma discoid (rarely deltoid in <i>S. densiflora</i> ).
Petal base dilated and usually denticulate.	Petal base entire, not dilated.
Species predominantly gypsophilous.	Species not gypsophilous.

It is unfortunate that only one of the three species of *Synthlipsis* has been available for cytological and chemical analysis, but *S. densiflora* and *S. elata* are known only from the type collections (Rollins, 1959). Nevertheless, the occurrence of  $n = 10$  in *S. greggii* together with a flavonoid pattern similar to that found in *Nerisyrenia johnstonii*, *N. castillonii* and *N. turneri*, all of which appear



to be based on  $x = 10$ , further emphasizes the close relationship between the two genera. Indeed, it might well be argued that the differences enumerated above are merely “technical”, and the two taxa might best be treated as a single genus. But, in a family where generic limits are often “arbitrary” and based “more on tradition than conviction” (Rollins, 1959, 1960, 1962; Rollins & Shaw, 1973), the morphological distinctions presented above would seem sufficient to mark them as genera.

#### PHYLOGENY

In attempting to reconstruct the phylogeny of *Nerisyrenia*, I have experienced considerable difficulty in determining the ancestral and derived state of morphological characters. This difficulty is, apparently, commonly encountered within the Cruciferae and stems, perhaps, from the fact that many genera, and species within genera, are the “end points of several evolutionary lines” in which intermediate groups are extinct; the “reading” of evolutionary trends is, thus, made difficult (Rollins & Shaw, 1973; Shaw, 1972). Moreover, the “evolutionary stimuli” which have molded the present species of *Nerisyrenia*, primarily extreme aridity and diverse edaphic and topographic settings, are those “stimuli” under which morphological relationships might well be obfuscated, due to relatively rapid divergence with concomitant morphological changes (cf. Stebbins, 1952; Raven, 1964), or misleading, due to parallelisms and associated morphological convergence (cf. Tucker, 1974; Went, 1971). Indeed, I believe that such events have occurred in the history of *Nerisyrenia*; consequently, in constructing the phylogeny of *Nerisyrenia*, I have considered cytological and distributional data and the geological history of the occupied area. I have also relied on the flavonoid data which suggest species relationships and further indicate two evolutionary lines within the genus. In treating the phylogeny of the group, I recognize the two chemical lines as distinct, although no formal taxonomic recognition is accorded them since similar morphological expressions are found in each grouping.

In order to visually express my concept of the relationships of the species of *Nerisyrenia*, I have adopted the “Wagner Divergence Index” (Wagner, 1971; see Hardin, 1957); under this scheme, a numerical value of 0 or 1 is given to those character expressions pre-



sumed to be "primitive" or "advanced", respectively. Intermediate character states may be assigned a value of 0.5. The summation of these value assignments for each taxon then represents a numerical expression of the degree of advancement of that taxon from the hypothetical, "primitive" state. These summations may then be plotted on a set of concentric rings to portray a "phyletic tree" for the genus. Listed below are the characters which I feel are useful as phylogenetic indicators and the expressions or state of the characters which I presume to be ancestral or derived; I have based my assumptions on an assessment of the distribution of these character states within *Nerisyrenia* and the related genus *Synthlipsis*:

CHARACTER	STATE	
	<i>Ancestral</i>	<i>Derived</i>
1. Fruit shape	obcompressed	terete (compressed)
2. Fruit apex	notched	entire
3. Habit	herbaceous	suffruticose
4. Root	taproot	rhizomatous
5. Leaf shape	broad	linear-spathulate
6. Leaf margin	not entire	entire
7. Vestiture	pubescent	glabrous
8. Base chromosome number	$x = 10$	$x = 9$

The evaluation of these character states for each taxon is given in Table V; the degree of advancement of each taxon is shown in Figure 2.

The relationships illustrated in Figure 2 are based largely upon morphology, although chemical evidence has been utilized in the recognition of this dichotomy. Some minor chemical incongruities exist in the line in which *Nerisyrenia incana* is basal; indeed, a better "chemical phylogeny" would result by assuming that *N. powellii* and *N. castillonii* are the more "primitive" taxa, a reversal of that proposed on morphology. This suggestion arises from the fact that *N. johnstonii*, *N. castillonii* and *N. turneri* all utilize glucose and galactose as glycosidic constituents. In the other grouping, the species considered "primitive" on morphological grounds do not utilize galactose, whereas galactosides occur sporadically in the more advanced taxa and become quite frequent in the most advanced species. If it is assumed that the original ancestor of



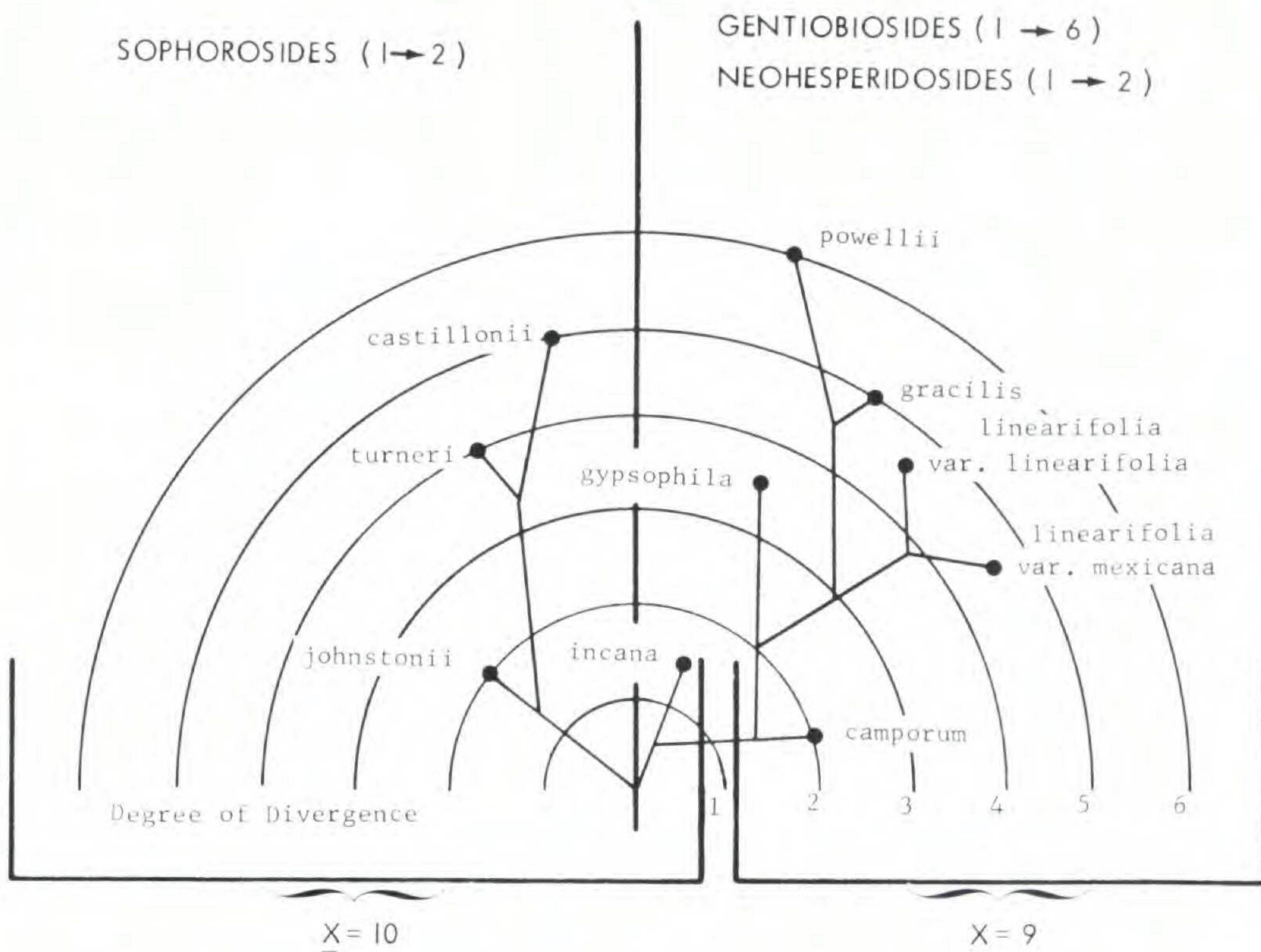


Figure 2. Diagram of species relationships in *Nerisyrenia*.

*Nerisyrenia* had the ability to produce both types of glycosides, then one might expect this ability to be retained in the more primitive species. This assumption would favor *N. powellii* and *N. castillonii* as the most primitive species. Furthermore, by assuming that the former species are primitive, one finds a progressive decline in the ability to produce galactosides in the "powellii" line, resulting in a decrease in the complexity of the flavonoid profile, while a similar trend is seen in the "castillonii" line, since *N. johnstonii* would then be an advanced taxon, and it lacks the ability to produce the triglycosides characteristic of *N. turneri* and *N. castillonii*. Under this scheme, the trend in flavonoid chemistry would support the generality proposed by Mabry (1973) that within a genus reduction in the complexity of the secondary products chemistry, reflecting a loss of biosynthetic ability, is indicative of evolutionary advancement. Such trends have been noted in several genera of plants including *Vernonia* (Compositae) (Mabry *et al.*, 1975; Abdel-Basset, 1973), *Linum* (Linaceae) (Gianassi & Rogers, 1970), *Ulmus* (Ulma-



Table V.

Divergence Index Values for Species of *Nerisyrenia*

	camporum	incana	gypsophila	powellii	gracilis	linearifolia linearifolia	linearifolia mexicana	johnstonii	castillonii	turneri
1. Fruit shape	0.0	0.0	0.0	1.0	1.0	0.5	0.5	0.0	1.0	1.0
2. Fruit apex	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0
3. Habit	0.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	1.0	0.0
4. Root	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0
5. Leaf shape	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0
6. Leaf margin	0.0	0.5	0.5	1.0	1.0	1.0	1.0	1.0	0.0	0.0
7. Vestiture	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0
8. Basic chromosome number	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0
TOTAL	2.0	1.5	3.5	7.0	6.0	5.5	5.5	2.0	5.0	4.0

ceae) (Bate-Smith & Richens, 1973), *Geranium* (Geraniaceae) (Bate-Smith, 1973), *Chamaesaracha* (Solanaceae) (Averett, 1970) and *Oenothera* (Onagraceae) (Howard, 1971). However, Harborne (1967) takes a contrasting view and suggests that increasing complexity of glycosylation patterns is indicative of evolutionary advancement; such has been shown to be the case in *Baptisia* Harborne, 1971; Turner, 1969, 1971). Both the above phenomena have occurred in the evolution of the species in *Lasthenia* (Compositae) and *Pyrus* (Rosaceae) (Bohm, Saleh & Ornduff, 1974; Challice & Westwood, 1973). The chemical phylogeny proposed for *Nerisyrenia* flavonoids, on morphological grounds, would fit into the evolutionary scheme proposed by Harborne.



Since the chemical evidence varies somewhat from my interpretation of the morphological trends, I present below the evidence leading to the acceptance of *Nerisyrenia incana* and *N. johnstonii* as the most "primitive" species within the genus.

Both *Nerisyrenia johnstonii* and *N. incana* are localized endemics in south-central Coahuila. The latter occupies the Cuatro Ciénegas Basin and extends further south in the valleys leading away from the central basin; the former is known from only a single locality approximately two kilometers west of the small ejido of Las Delicias, Coahuila, which is approximately 80 miles southwest of Cuatro Ciénegas.

The area occupied by *Nerisyrenia incana* is unusual for the Chihuahuan Desert as it supports several natural streams and ponds; those areas with constant water support aquatic to semi-marsh vegetation (Meyer, 1973; Minckley, 1969; Gilmore, 1947). However, *N. incana* never occurs in the wet areas and is limited to the arid gypseous dunes or saline flats of the area. The single site occupied by *N. johnstonii* appears to be a more mesic habitat, and the species is limited to the area around a natural spring. While the spring has been diverted recently by a concrete aqueduct to supply water to the village of Las Delicias, a deep arroyo, approximately 100 feet deep, attests to the former direction of flow of the spring effluent.

These species share general morphological similarities such as fruit shape, leaf form, a tendency for the fruits to be congested toward the raceme apex, and they also share a diploid chromosome number of  $n = 10$ . The apical notch of their fruits is found in no other species of *Nerisyrenia* but is present in all species of the related genus *Synthlipsis*; the only species of *Synthlipsis* known chromosomally also has a chromosome number of  $n = 10$  (Rollins, 1966; this study). On morphological grounds, both species are somewhat "isolated" from the other members of their respective lines, especially in their fruit morphology, suggesting, perhaps, that they are "old" species, now relict in their distribution (cf. Stebbins & Major, 1965). It is noteworthy that the only perennial species of *Synthlipsis*, *S. densiflora*, also has a more congested raceme than the other species of *Synthlipsis* and is known only from limestone bluffs on the southwest corner of the Sierra de la Fragua, the same mountain complex in which *N. johnstonii* occurs.



However, the largely polyploid chromosome numbers for *Nerisyrenia castillonii* and *N. powellii*, the diploids either rare or unknown, imply a considerable age for these taxa (cf. Stebbins & Major, 1965). Under such an assumption, *N. johnstonii* and *N. incana* would have to be considered as derived, and then the origin of *N. johnstonii* poses a problem. On morphological grounds, derivation of *N. johnstonii* directly from *N. castillonii* does not seem feasible. An origin for *N. johnstonii* from some now extinct diploid progenitor must be inferred.

No such problem exists as regards *Nerisyrenia incana* since a possible diploid progenitor exists in *N. camporum*. In this case, however, one must assume an aneuploid gain in chromosome number, a possible event (Lewis & Roberts, 1956; see Walker, 1972; Stebbins, 1971, p. 18), although, in plants, not as common as aneuploid loss (see Brown, 1972, for discussion of both types of change); and one must assume the morphological similarities between *N. incana* and *N. johnstonii* are the result of parallel evolution. Clearly, parallelisms in habit, fruit shape and root type have occurred in *Nerisyrenia*, but where these parallelisms have occurred, e.g., between *N. castillonii* and *N. powellii*, and to a lesser extent, between *N. gracilis* and *N. turneri*, the species concerned exist under very similar environmental conditions. The apparent habitat differences between *N. incana* and *N. johnstonii* would seem to negate a strong argument for parallelism, and their similarities seem best considered as indicative of their origin from now extinct, ancestral stocks of *Nerisyrenia*.

The Cuatro Ciénegas Basin has received a relatively large amount of attention from biologists due to its unique permanent water system. The aquatic habitats of the basin harbor a number of endemic fishes and snails, while the terrestrial fauna includes several endemic scorpions and reptiles; many of the endemic species are considered to be relicts (Meyer, 1973; Minckley, 1969; Cole, 1968, p. 476; Miller, 1968; Taylor, 1966; Hubbs & Miller, 1965; Webb, Minckley & Craddock, 1963). The aquatic habitats of the area are inferred to be geologically old and stable; Taylor (1966) has postulated an early to mid-Tertiary isolation for the ancestral stock of the snail fauna and suggests the valley itself, or at least the aquatic habitats, is no younger than Pliocene and may be as old as early Oligocene in age. Miller (1968) suggests an early Pliocene-late Miocene isolation for some of the fishes in the area.



The recent work of Meyer (1973) would also lend support to the suggestion that environmental stability has long characterized the Cuatro Ciénegas Basin. Meyer (1973) has shown, by examination of fossil pollen profiles cored from the valley floor, that the vegetation occupying the basin floor during mid-Wisconsin time, ca. 40,000 years ago, was essentially the same as it is today. There was a vertical lowering of the vegetation now restricted to the higher elevations of the surrounding mountains, suggesting cooler, perhaps moister conditions, as recorded for other areas in the northern Chihuahuan Desert (Martin & Mehringer, 1965; Wells, 1966; Flint, 1971, pp. 503–506), but the descending woodland did not invade the valley floor. Meyer suggests that the unique gypseous-saline edaphic conditions of the basin floor prevented such an invasion. These results, too, render invalid the suggestion by Minckley (1969) and Cole (1968, p. 476) that the basin was covered by a large Pleistocene lake(s). Implicit from these results is the inference that the floor of the Cuatro Ciénegas Basin has been a stable habitat throughout Quaternary time, perhaps longer, and was essentially unaffected by the climatic changes wrought by the glacial periods.

The age of the Cuatro Ciénegas Basin may be estimated as middle Pliocene since the mountains surrounding the basin are part of the Sierra Madre Oriental (Gilmore, 1947; King, 1935) which was uplifted during that period (Garfias & Chapin, 1949; Schuchert, 1935). The area has been available for occupation for a long period of time, and under the stable conditions inferred for the basin, one might expect to find populations not greatly changed from their ancestral state.

The evidence presented above, showing that *Nerisyrenia incana* and *N. johnstonii* share morphological similarities (some of which are also found in the related genus *Synthlipsis*), thought not to be due to parallelism, that they share a diploid chromosome number of  $n = 10$  (also found in *Synthlipsis*), and that they occupy a relatively old and stable habitat, strongly suggests that these species are “primitive” as suggested in Figure 2.

The origin of *Nerisyrenia* clearly was in Mexico; the concentration of the diploid populations, the representation of all species in Mexico and the presence of ancestral types in this region make any other origin very unlikely. The age of the taxon is less certain, as it is in any group in which fossil evidence is unavailable. However,



the Cruciferae was certainly evolving by Oligocene time since fossil fruits referable to the genus *Thlaspi* have been found in an upper Oligocene flora from the Ruby River Basin in Montana (Becker, 1961). Also, fossil pollen belonging to the family has been reported from Cretaceous deposits in New Zealand (see Rodman, 1974), pointing to an even earlier origin for the family. The evidence previously presented indicates that the area occupied by the "most primitive" species in the genus was available for occupancy by mid-Pliocene time. It is also apparent that *Nerisyrenia* has evolved in response to increasing aridity and edaphic diversity, and arid conditions did not become regional features until late Pliocene (Axelrod, 1950, 1958, 1970). Certainly, the uplifting of the Sierra Madre Oriental accelerated the trend toward aridity in the eastern portions of the Chihuahuan Desert. The distribution of *Nerisyrenia* suggests that it has kept pace with this development of aridity. Considering all this evidence, I would suggest that the genus probably had a Pliocene origin.

The ancestors of *Nerisyrenia* probably were located in the east-central portion of the present Chihuahuan Desert and existed under relatively more mesic conditions. The uplift of the Sierra Madre Oriental brought increasingly arid conditions to the region, resulting in widespread extinction of the ancestral group. Some populations persisted, however, in locally mesic habitats, as represented today by *N. johnstonii*. Other populations expanded under the increasing aridity, perhaps due to their previous occupation of localized "dry spots", therefore, being somewhat pre-adapted to the arid conditions (cf. Axelrod, 1950, 1967, 1972); these populations may have been somewhat divergent from the larger body of the ancestral stock, at least in their flavonoid chemistry, and the net result of this early evolutionary period was the establishment of the two "chemical lines" present today.

In the "incana" line, a reduction of chromosome number from  $x = 10$  to  $x = 9$  occurred. The more aggressive  $x = 9$  stock expanded, and the  $x = 10$  populations were restricted in range, as represented today by *Nerisyrenia incana*.

As the  $x = 9$  line expanded in range, it encountered numerous localized areas where unique edaphic factors, such as gypsum, were present. In the expanding population, some individuals were pre-disposed towards this restrictive soil type and became established. These individuals subsequently were isolated due to the withdrawal



of the larger body of the progenitor populations in response to local climatic fluctuations such as extended localized drought (cf. Raven, 1964; Lewis, 1966). The derivative populations then diverged, the colonizers themselves being, perhaps, somewhat divergent from the "typical" ancestors, under the combined effects of selection and drift and left *N. gypsophila*. Alternatively, the derivative populations may have diverged under conditions of neighboring sympatry through disruptive selection (cf. Antonovics & Bradshaw, 1970; McNeilly & Antonovics, 1968; Murray, 1972, pp. 87-110; Grant, 1971, pp. 119-122).

The rhizomatous species of the "incana" line are thought to have had their origin in a similar event. *Nerisyrenia linearifolia* is viewed as arising in some localized gypseous area in the central Chihuahuan Desert; it subsequently spread north and south, and regional selection pressures caused the divergence of the two varieties.

The progenitor population(s) of *Nerisyrenia powellii* and *N. gracilis* probably arose as a later offshoot from the "stock" which gave rise to *N. linearifolia*. As these populations diverged from their ancestors, they were able, also, to expand their range, but their emigration was primarily to the south. Again, regional differences in selection pressures resulted in the divergence of the ancestral group into *N. powellii* and *N. gracilis*.

A similar history is envisioned for the "johnstonii" line with similar evolutionary events having occurred. The products of these speciation events were "less successful", however, than those of the "incana" line, and today, only the three species remain.

#### ACKNOWLEDGMENTS

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## TAXONOMY

**Nerisyrenia** Greene, *Pittonia* 4: 225. 1900. *Nom Nov.* Based on *Greggia* A. Gray.

*Greggia* A. Gray, *Smithson. Contrib. Knowl.* 3(5): 8. 1850, non Gaertn. 1788, nec. Engelman, 1848. TYPE: *G. camporum* A. Gray.

*Parrasia* Greene, *Erythea* 3: 75. 1895, non Raf., 1847. *Nom. Nov.* Based on *Greggia* A. Gray.

Suffruticose or herbaceous, often rhizomatous perennials, 0.5 to 6.0 dm tall, pubescent throughout (glabrous in one species), densely to moderately so, with sessile to long-stalked, dendritically branched trichomes. Stems few to many from a usually woody taproot or caudex, upright, ascending to decumbent, branching freely or the branching somewhat restricted. Leaves 10–84 mm long, 1–40 mm broad, terete to flattened, often succulent; linear, oblanceolate, spatulate to elliptic in outline, attenuate-subpetiolate at base, acute to obtuse at apex; margins entire, repand to markedly dentate, weakly revolute in some. Inflorescence racemose, elongating in fruit. Sepals 5–10 mm long, 1–3 mm broad; linear-oblong, lanceolate to oblanceolate in outline, non-saccate, acute to obtuse at apex; margins scarious; spreading at anthesis, reflexing with age. Petals flaring just prior to anthesis, 8–16 mm long, 4.5–9.0 mm broad, white, often fading lavender; the blade obovate, spatulate to broadly elliptic, narrowing rather abruptly to a short claw, the claw dilated and denticulate at base; margins of the blade entire; the midnerve and its branches often yellow in lower 1/3–1/2 of petal. Stamens 5–9 mm long, exserted, divergent; anthers 2–4 mm long, introrse, sagittate, curling with age; filaments 4.0–7.5 mm long, terete to slightly flattened, glandular tissue present, subtending the filaments. Infructescence 4–45 cm long, included to well exserted above the leaves, lax to congested; pedicels 5–20 mm long, expanded at the apex, divaricately ascending to recurved. Siliques 6–40 mm long, 1–9 mm wide, linear-oblong to obovate in outline, terete, compressed or obcompressed, straight, curved to tortuous; valves obtuse-truncate to acute at apex, obtuse at base, with an often obscured single lateral line from base to apex, not carinate. Style persistent, 1.5–6.5 mm long, glabrous. Stigma 0.4–1.5 mm long, sagittate-deltoid, somewhat decurrent on the style. Replum 0.5–3.6 mm broad; septum entire, translucent, with a prominent nerve extending from base to apex. Seeds numerous, 40–100 per fruit; 1.2 mm or less long, less than 1 mm broad; ovate-elliptic to



oblong, plump to slightly flattened; wingless; seed coat slightly roughened, yellow to yellow-brown; cotyledons incumbent. TYPE SPECIES: *Nerisyrenia camporum* (A. Gray) Greene.

#### KEY TO THE SPECIES

1. Broadest leaves 8 mm broad or more. . . . . 2.
2. Plants glabrous, or with a few dendritically branched trichomes along the leaf margin. . . . . 1. *N. johnstonii*.
2. Plants pubescent, the pubescence moderate to dense. . . . . 3.
3. Siliques markedly obcompressed, valves rounded truncate at apex. . . . . 4.
4. Siliques 4–9 mm broad, shallowly to deeply notched at apex, valves extending 0.5–1.5 mm past insertion of style; plants woody, pubescence incanous. . . . . 4. *N. incana*.
4. Siliques rarely 4 mm broad, rarely shallowly notched at apex; plants green to gray, never incanous. . . . . 5.
5. Replum 1.1 mm broad or less; pedicels of fruit rather rigidly ascending, never recurved; silique never strongly curved; plants suffruticose. . . . . 6. *N. gypsophila*.
5. Replum 1.0–1.4 mm broad; pedicels ascending to divaricately spreading or recurved; silique straight to strongly curved inward, in conjunction with pedicel, often sigmoid; plants not suffruticose. . . . . 5. *N. camporum*.
3. Siliques terete-subterete or somewhat compressed, valves tapering to the style. . . . . 6.
6. Plants arising from a woody taproot or rhizome, never appearing tufted or caespitose; leaves 7–22 mm broad; styles 3.5 mm long or longer; plants suffruticose. . . . . 3. *N. castillonii*.
6. Plants usually arising from a slender rhizome, usually appearing caespitose; leaves 4–8 mm broad; styles usually less than 3.8 mm long. . . . . 2. *N. turneri*.
1. Broadest leaves less than 8 mm broad. . . . . 7.
7. Plants suffruticose. . . . . 8.
8. Siliques strongly obcompressed, valves rounded truncate at apex, replum 1 mm broad or less. . . . . 6. *N. gypsophila*.
8. Siliques terete to compressed, valves tapering to the style. . . . . 9. *N. powellii*.
7. Plants not suffruticose. . . . . 9.
9. Valves of siliques truncate-rounded at apex, or if rarely tapering to the style then plants of the United States. . . . . 7. *N. linearifolia*.
9. Valves of siliques tapering to the style; plants of Mexico. . . . . 10.
10. Infructescence rarely exceeding the leaves but if so then the siliques tortuous and valves papery; fruits slender, valves weakly to strongly constricted between the seeds; leaves usually less than 2.5 mm broad with entire margins. . . . . 8. *N. gracilis*.
10. Infructescence usually exceeding the leaves; fruits not slender, valves rarely constricted between the seeds; leaves mostly over 2.5 mm broad with sinuate to dentate margins. . . . . 2. *N. turneri*.



1. ***Nerisyrenia johnstonii*** Bacon sp. nov. TYPE: **México.**

COAHUILA: about 1 km W of Las Delicias at and near spring, top of alluvial fan on side of mountain, 24 Mar 1973, *M. C. Johnston, T. L. Wendt & F. C. Chiang 10388*. (Holotype, TEX!; Isotypes, to be distributed.)

Herbae perennes ad 6 dm altae radice palari radicatae glabrae praeter omnino raro margines foliorum. Caules plures vel multi erecti vel modice effusi. Folia succulenta lanceolata vel oblanceolata subpetiolata apice obtusa vel acuta margine integra vel interdum sinuato-dentata leniter undulata, inferiora 40–60 mm longa 15–25 mm lata. Sepala 4.5–7.0 mm longa 1.5–2.5 mm lata, subulata vel oblanceolata apice acuta vel obtusa demum effusa. Petala 8–11 mm longa 5–8 mm lata, late obovato-spathulata apice obtusa base dilatata. Stamina 6.5–9.0 mm longa, filamenta 4–6 mm longa, antherae 2.5–3.0 mm longae. Infructescentia 15–30 cm longa supra folia plane exserta congesta; pedicelli 9–15 mm longi base admodum recte adscendentes, apicem versus aliquantum effusi, inferiores remoti superiores congesti. Siliquae 10–15 mm longae vel infimae interdum tantum 5 mm longae 5–9 mm latae, ellipticae vel oblongae vel late ovatae obcompressae, apice integrae vel retusae; valvae leviter corrugatae apice rotundatae. Stylus conspicuus 2.5–4.0 mm longus. Stigma deltoideo-sagittatum in stylo leniter decurrens saepe leviter bilobatum. Replum 1.2–1.6 mm latum oblongum. Semina ca. 80 vel in siliquis parvulis pauciora, 0.6–0.8 mm longa 0.4–0.5 mm lata ovata turgida flava. Chromosomatum numerus:  $2n = 20$ .

DISTRIBUTION: Presently known only from the type locality near Las Delicias, Coahuila (Figure 3).

REPRESENTATIVE SPECIMENS: **México.** COAHUILA. 1 km W of Las Delicias, *Bacon & Dillon 1478* (TEX), *Powell & Turner 2702* (TEX).

*Nerisyrenia johnstonii* because of its lack of pubescence is the most distinctive taxon in the genus. Its affinities reside with *N. turneri* and *N. castillonii*, as indicated by its chromosomal base ( $x = 10$ ) and flavonoid chemistry. Nevertheless, on morphological grounds the latter species are well differentiated, and this relationship must be viewed as somewhat distant. Indeed, *N. johnstonii* is thought to be among the more “primitive” species of the genus while *N. turneri* and *N. castillonii* are thought to be among the more highly “evolved”.



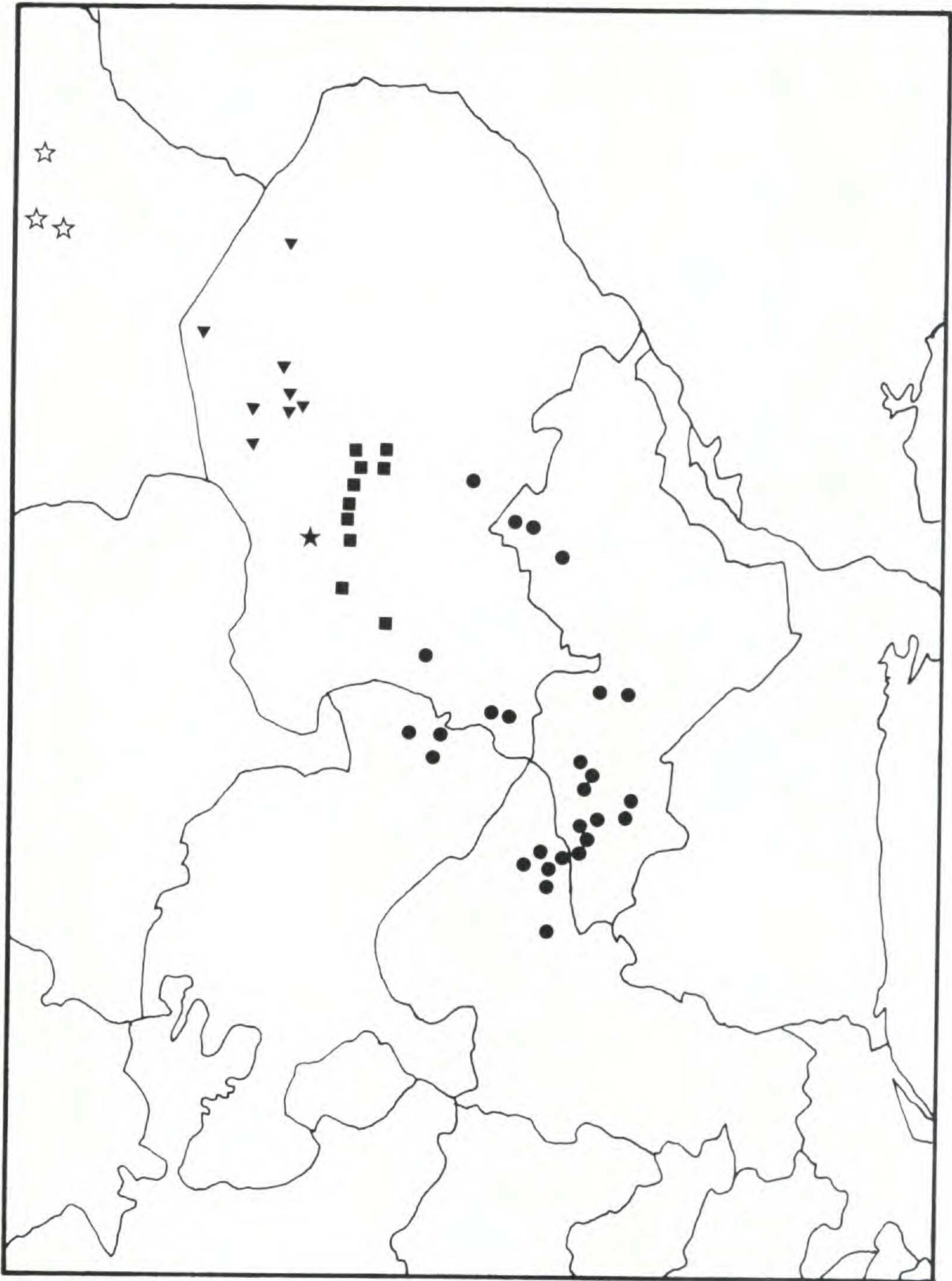


Figure 3. Distribution of species of *Nerisyrenia*: *N. gracilis*, closed circles; *N. gypsophila*, open stars; *N. johnstonii*, closed star; *N. incana*, closed squares; *N. powellii*, closed triangles.



Morphologically, *Nerisyrenia johnstonii* resembles *N. incana* and they share a base chromosome number of  $x = 10$ . However, the two are readily distinguished, the former being herbaceous and glabrous while the latter is suffruticose and incanous pubescent. Because the flavonoid chemistry of the two is very distinctive, *N. johnstonii* is clearly allied with *N. turneri* and *N. castillonii*, both of which appear to be based on  $x = 10$ , and *N. incana* is allied with the remaining taxa in the genus, all of which have  $x = 9$ . Therefore, the morphological resemblance between the two species is thought to reflect the "primitive" nature of the taxa, their similarities indicating the retention of morphological characters more prevalent in the ancestral stock of the genus.

The name honors Dr. M. C. Johnston, noted student of the Chihuahuan Desert flora, who first brought this remarkable taxon to my notice.

2. ***Nerisyrenia turneri*** Bacon sp. nov. TYPE: **México**. SAN LUIS POTOSÍ: 5/10 mile west of Jct. Hwy. 101 & 80; along roadside in sandy-loamy, gypseous soil, 24 Jun 1971, *John D. Bacon 983*. (Holotype, TEX!; Isotypes, to be distributed.)

Herbae perennes rhizomatosae 0.5–3.0 dm altae; caules plures erecti vel adscendentes modice pubescentes trichomatibus sessilibus vel brevistipitatis dendriticis. Folia 20–70 mm longa (2–)4–8(–10) mm lata, lineari-oblongata raro elliptica, subsucculento-incrasata saepe planata apice acuta vel subacuta basi attenuata margine sinuosa vel dentata raro integra, super dentes elongata angustataque ubi dentata. Sepala 5.0–7.5 mm longa 1.0–2.2 mm lata, oblonga vel lanceolata vel oblanceolata, apice acuta vel obtusa modice vel dense pubescentia trichomatibus sessilibus vel brevistipitatis dendriticis. Petala 6–9 mm longa 5–8 mm lata, laminis obovatis vel anguste ellipticis edentatis, basibus dilatatis denticulatis. Stamina 7–10 mm longa, filamenta 5.5–7.5 mm longa, antherae 2.5–3.5 mm longae. Infructescentia 4–10 cm longa base inter folia inclusa vel non inclusa. Pedicelli 7–15 mm longi divaricate adscendentes vel recurvati. Siliquae 11–26 mm longae 1.2–2.0 mm latae teretes vel raro compressae rectae vel valde arcuatae; valvae aliquantum crassae, raro inter semina constrictae, apicem versus gradatim contractae, apice acutae vel subacutae. Stylus 2.5–3.8 mm longus glaber. Stigma 0.7–1.5 mm latum deltoideo-sagittatum aliquantum super



stylum decurrens. Replum 1.0–1.5 mm latum. Semina 50–80, 0.6–1.0 mm longa, 0.5–0.8 mm lata, ovata vel elliptica vel oblonga flavo-brunnea. Chromosomatum numerus:  $2n = 20, 32, 33, 36, 38$ .

**DISTRIBUTION:** Plants limited to southern Nuevo León and northern San Luis Potosí (Figure 4), in sandy-gravelly alluvial gypsum soils or crusty, exposed gypsum flats. Flowering from March to September.

**REPRESENTATIVE SPECIMENS:** **México.** NUEVO LEÓN: 1 mi S of Providencia on Hwy 57, *Bacon & Dillon 1487* (TEX); 14.3 mi N of San Roberto, *Bacon 1017* (TEX); 17 mi S of San Roberto on Hwy 57, *Bacon, Leverich & Turner 1115* (TEX); just W of Hwy 57 on road to Cedral, *Bacon, Leverich & Turner 1127* (TEX). SAN LUIS POTOSÍ: 1/10 mi E of Hwy 57 on road to El Refugio, *Bacon 996* (TEX); 27.6 mi S of Matehuala on Hwy 57, *Bacon & Dillon 1493* (TEX); 42.5 mi S of Matehuala on Hwy 57, *Bacon & Dillon 1494* (TEX); 9 mi NW of Huizache Jet on Hwy 57, *Bacon & Hartman 1333* (TEX); 36.5 mi E of Huizache Jet on Hwy 80, *Bacon & Dillon 1495* (TEX); jct Hwy 101 and 80, *Bacon & Hartman 1330* (TEX); 4.7 mi E of jct Hwy 101 and 80, *Bacon 981* (TEX); 5.3 mi E of jct Hwy 101 and 80, *Bacon & Dillon 1497* (TEX); 10.5 mi E of jct Hwy 101 and 80, *Bacon 982* (TEX); 11 mi E of jct Hwy 101 and 80, *Bacon & Hartman 1329* (TEX).

This species is related to *Nerisyrenia castillonii* (see comments under that taxon) but is easily separated from it.

The distribution of *Nerisyrenia turneri* overlaps, to some extent, with that of *N. gracilis*. While the two species are clearly differentiated, morphologically extreme plants of one taxon may resemble, superficially, plants of the other. In order to alleviate any confusion which might result, the following list of differentiating characters is presented:

<b>N. turneri</b>	<b>N. gracilis</b>
Leaves: 4–8 mm broad; margins sinuate-dentate.	0.7–2.5 mm broad; entire.
Siliques: 1.2–2.0 mm broad.	0.7–1.3 mm broad.
Valves: rather “thick”, rarely constricted between the seeds.	Thin, commonly constricted between the seeds.

This taxon is named for Dr. B. L. Turner whose encouragement, love of plants and appreciation of living are inspirational.

3. ***Nerisyrenia castillonii*** Rollins, *Contr. Dudley Herb.* 3: 181.

**TYPE:** **México.** COAHUILA: confined to gypsum flats, common



locally; forming depressed, rounded clumps, leaves fleshy, petals white; near corrals of the hacienda Castillon, ca lat. 28° 17' N, 15 Sep 1940, *I. M. Johnston & C. H. Muller 1264* pro parte. (Holotype, GH! (exclude lower member on sheet = *N. powellii* Bacon); Isotype, TEX!).

Perennial subshrub, 2–4 dm high; stems several to many from a woody taproot or rhizome, erect to subdecumbent, younger stems densely pubescent, canescent to incanous, with sessile and short- to long-stalked, dendritically branched trichomes, the pubescence often appearing tufted; older stems often glabrate. Leaves commonly, somewhat thickened-succulent, rarely thin, 20–60 mm long, 7–20 mm broad, oblanceolate to narrowly oblong-elliptic in outline, attenuate-subpetiolate at base, obtuse to acute at apex; margins rarely entire, usually repand to strongly dentate, often the leaf narrowed and elongated past the final dentations; densely pubescent with sessile or short-stalked dendritically branched trichomes and scattered longer stalked hairs. Petals 9–12 mm long, 5–8 mm wide; obovate-narrowly elliptic, margins entire to somewhat undulate, dilated and denticulate at base, but often the dilation narrow and denticulations absent. Stamens 7–10 mm long; filaments 5.5–7.5 mm long, anthers 2.8–3.5 mm long. Infructescence rather lax, not stout, 7–30 cm long, usually prominent above the leaves; pedicels 6–12 mm long, densely pubescent, ascending, divaricately spreading to declinate, rather uniformly spaced throughout, not densely congested towards apex. Siliques (13–)20–40 mm long, 1–2 mm broad, terete to subterete, commonly somewhat compressed parallel to the replum, straight, more commonly curved, often strongly so, to J-shaped, infrequently tortuous, often somewhat broader at the base than the apex; valves subacute to somewhat rounded at apex (rarely truncate) tapering to the style, not becoming manifestly thinner at maturity. Style manifest, (2.7–)3.5–6.0(–6.5) mm long, glabrous or rarely with a few scattered trichomes near the apex. Stigma 0.7–1.3 mm long, deltoid-sagittate, somewhat decurrent on the style. Seeds 40–80 (to ca. 100 in longer fruits) per silique, 0.7–1.3 mm long, subelliptic to ovate-oblong, plump to slightly flattened; yellow to tannish-yellow. Chromosome number:  $2n = 20, 40, 48, 58, 59$ .

**DISTRIBUTION:** Coahuila, occurring in gypseous clays and sandy alluvial gypsum soils of desert flats (Figure 4). Flowering March to October.



REPRESENTATIVE SPECIMENS: **México.** COAHUILA: 8.7 mi SE of Emiliano Zapata on road to Viesca, *Richardson 1661* (TEX); Sierra de Jimulco and up to 3 km N of Mina San José which is 8 km NE of Estación OTTO, *Chiang, Wendt & Johnston 9532a* (TEX); S end of Cañada Oscuro near Tanque la Luz, *I. M. Johnston 8498* (GH); western base of Picacho del Fuste, NE from Tanque Varionetta, about lat 27°34' N, *I. M. Johnston 8351* (GH, TEX); Noria, 16 mi S of Estanque, *Shreve 8842* (US); 36.1 mi N of San Pedro de las Colonias on Hwy 30, *Richardson 1658* (TEX); 24.2 mi N of San Pedro de las Colonias on Hwy 30, *Bacon 1023* (TEX); 55.3 mi S of Cuatro Ciénegas on Hwy 30, *Bacon 1036* (TEX); 45 mi S of Cuatro Ciénegas on Hwy 30, *Bacon & Dillon 1477* (TEX); ca. 40 mi S of Cuatro Ciénegas on Hwy 30, *Bacon, Leverich & Turner 1095* (TEX); 36 mi S of Cuatro Ciénegas on Hwy 30, *Bacon & Dillon 1474* (TEX); ca. 12 mi SW of Cuatro Ciénegas, *Bacon & Leverich 1145* (TEX); 12.4 mi S of Cuatro Ciénegas and 2 mi W, *Richardson 1645* (TEX); 4 mi SW of Cuatro Ciénegas, *Turner 6187* (TEX); 12 mi S of Cuatro Ciénegas, *Bacon 1034* (TEX); 4 mi E of Cuatro Ciénegas, *Leverich & Turner 25* (TEX); San Juan, ca. 18 mi E of Cuatro Ciénegas, *Turner 6206* (TEX); 6.9 mi W of Sacramento, *M. C. Johnston 2582* (GH); several miles NW of Puerto de las Monjas, *I. M. Johnston 8638* (GH, TEX); 33 mi N of Ocampo, *Bacon & Hartman 1278* (TEX); Castillón, *I. M. Johnston 8186* (GH); 76.3 mi W of Cuatro Ciénegas, *Bacon & Leverich 1151* (TEX); 20 mi SE of Esmeralda, *Henrickson 6999* (TEX); ca. 3 km S of Puerta de Sardinias, *M. C. Johnston et al. 12174* (TEX); west banks of Laguna del Rey, *Bacon & Leverich 1232* (TEX); Matrimonio Viejo, ca. lat. 27°6'N, *I. M. Johnston 9346* (GH, TEX); ca. 8 mi SSE of Jaco, exactly 8 road mi N of Estación Hormigas, *Henrickson 6933* (TEX); Hermanas, *Bacon & Hartman 1315* (TEX); 0.5 mi S of Estación Hermanas, *Turner & Leverich 26* (TEX); 5/10 mi S of Hermanas on Hwy 57, *Turner 6039* (TEX); just S of Hermanas, *Correll & Johnston 21289* (GH, TEX), *21288* (TEX); ca. 1 mi S of Estación Hermanas, *Powell & Turner 2262* (TEX); 1 mi S of Estación Hermanas, *Turner 6167* (TEX), *Turner 6011* (TEX), *I. M. Johnston 7067* (GH); ca. 1 mi S of Hermanas, *Bacon 1030* (TEX); 2 km S of Estación Hermanas, *Wendt, Chiang & Johnston 10139* (TEX); km 19 on Hwy 57, *Bacon 1027* (TEX).

*Nerisyrenia castillonii* is most closely related to *N. turneri*. They are similar in many morphological features, differing quantitatively in most, but are easily separated by habit. *Nerisyrenia castillonii* is suffruticose while *N. turneri* is herbaceous.

Rollins (1941b) suggested that this taxon was related to *Nerisyrenia camporum*. He was unaware, however, of the existence of *N. turneri* and did not have the cytological or chemical data utilized in this study. In all respects, *N. castillonii* and *N. camporum* are distinctive and any relationship between the two must be quite distant.

Morphologically, *Nerisyrenia castillonii* resembles *N. powellii*. On the basis of cytological and chemical evidence, however, the two taxa appear to belong to divergent evolutionary lines and are not closely related. Distinguishing characteristics are presented below:



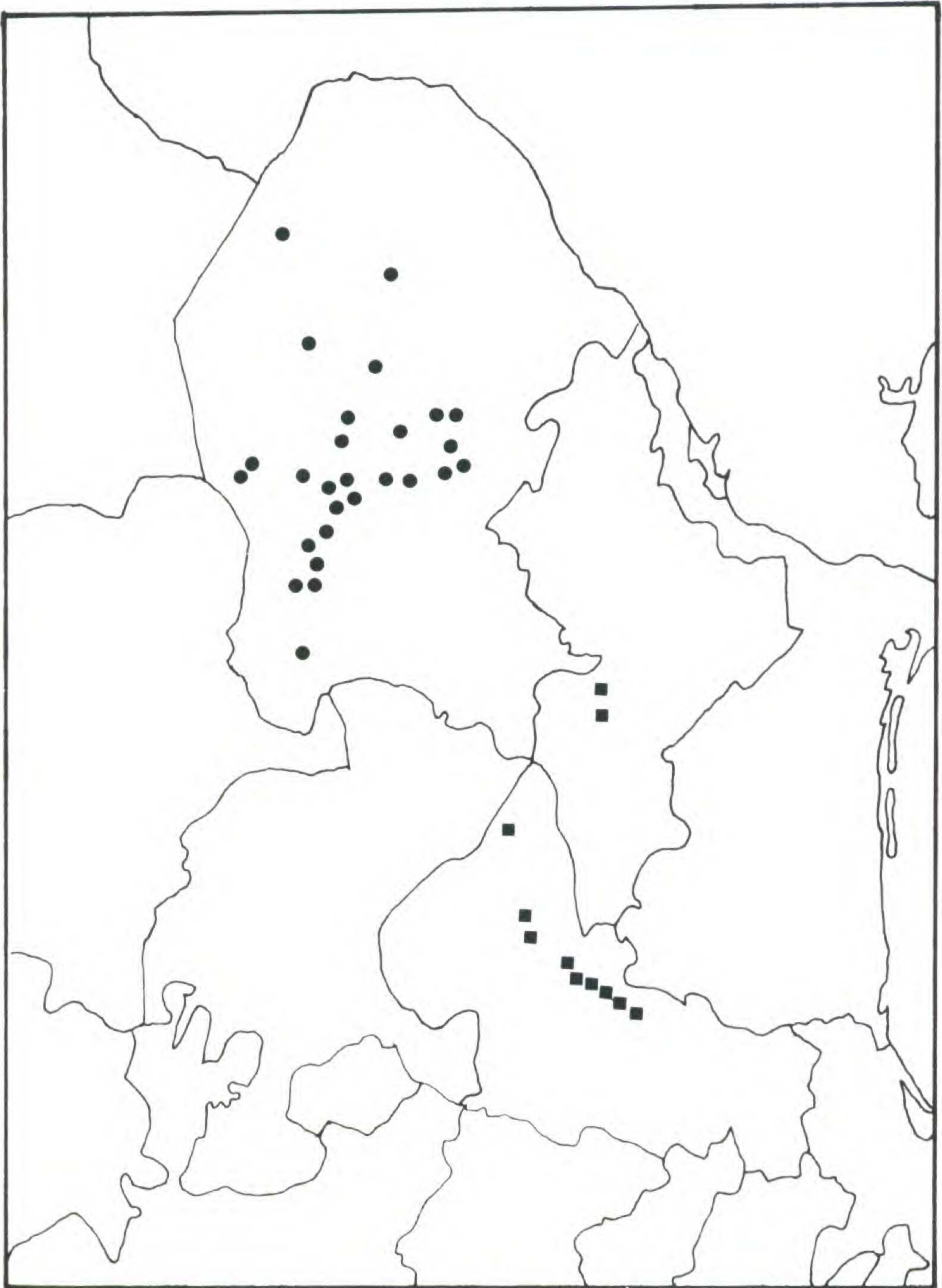


Figure 4. Distribution of species of *Nerisyrenia*: *N. castillonii*, closed circles; *N. turneri*, closed squares.



**N. castillonii**

Leaves: oblanceolate to oblong-elliptic; 7–20 mm broad.

Leaf margins: dentate-repand.

Style: 3.5–6.0 mm long.

**N. powellii**

Linear-spathulate; 2–5 mm broad.

Entire.

2.3–2.8 mm long.

4. **Nerisyrenia incana** Rollins, *Madroño* **5**: 132. 1939. TYPE: **México**. COAHUILA: infrequent in alkaline flats, perennial, petals white, associated with *Dondia*, 4 miles west of Cuatro Ciénegas, 24–26 Aug 1938, *I. M. Johnston 7130*. (Holotype, GH!).

Perennial subshrub to 6 dm tall, densely pubescent throughout, incanous, with short- to long-stalked dendritically branched trichomes, pubescence somewhat appressed on younger stems; stems several to many from a woody taproot; erect, somewhat spreading to ascending, branching freely; older stems to 1 cm thick with furrowed and somewhat exfoliating bark, often glabrate below. Leaves succulent-subsucculent, lower 43–84 mm long, 12–30(–40) mm broad, upper 22–42 mm long, 5–13 mm broad, oblanceolate to spatulate, occasionally obovate, obtuse to acute at apex, long to short attenuate at base (subpetiolate); margins entire to, not uncommonly, dentate, usually weakly revolute. Inflorescence elongating greatly in fruit, lower flowers often abortive. Sepals 7–10 mm long, 1.5–3.0 mm broad, linear-lanceolate to oblanceolate, rarely subulate, acute at apex, spreading at anthesis, becoming reflexed with age. Petals 9–16(–19) mm long; 5–8 mm broad, spatulate-obovate, obtuse at apex, margins entire, often weakly undulate, markedly dilated and usually denticulate at base. Stamens 6–9 mm long, filaments 4–7 mm long, anthers 3–4 mm long. Infructescence usually stout, 8–45 cm long, usually well exerted above the leaves; pedicels ascending to spreading at right angles to the axis, stoutish, rather widely spaced on lower 1/3 of axis, moderately to densely crowded on upper portion. Siliques 9–19 mm long, 4–9 mm broad, narrowly obovate to broadly oblong, obcompressed, shallowly to deeply notched at apex, valves extending 0.5–1.5 mm past insertion of the style, rounded-truncate at apex, inner surface of valves often finely pubescent with stalked, dendritically branched hairs. Style prominent, glabrous 2.5–4.7(–5.2) mm long. Stigma 0.8–1.5 mm long, sagittate-deltoid to rather cy-



lindrical, somewhat decurrent on the style. Replum 1.5–3.6 mm broad. Seeds 50–90 per silique, 0.7–1.0 mm long, 0.5–0.7 mm broad, ovate-elliptic-oblong, plump to slightly flattened; brownish-yellow. Chromosome number:  $2n = 20, 21, 22, 23$ .

**DISTRIBUTION:** A restricted gypsum endemic found only in the region of Cuatro Ciénegas in south-central Coahuila (Figure 3), occupying areas of pure gypsum sands or highly gypseous alluvial soils. Flowering from March to October.

**REPRESENTATIVE SPECIMENS:** **México.** COAHUILA: a mile W of Antejo, W of Cuatro Ciénegas, *I. M. Johnston 8865* (GH, TEX); 3 km SW of Cuatro Ciénegas, *Chiang, Wendt & Johnston 7616* (TEX); 2 mi S of Cuatro Ciénegas, *Bacon, Leverich & Turner 1088* (TEX); ca. 3 mi S of Cuatro Ciénegas, *Bacon & Leverich 1147* (TEX); 4 mi S of Cuatro Ciénegas on Hwy 30, *Bacon 1035* (TEX); 5 mi S and 2 mi E of Cuatro Ciénegas, *Bacon, Leverich & Turner 1084* (TEX); 16 km S of Cuatro Ciénegas, about 2 km SW of Pozo y Balneario La Becerra, *Johnston, Wendt & Chiang 10333* (TEX); 19 km SW of Cuatro Ciénegas, *Chiang, Wendt & Johnston 7644* (TEX); ca. 12 mi S and 5 mi NW of Cuatro Ciénegas, *Bacon, Leverich & Turner 1091* (TEX); W side of gypsum dunes ca. 12 mi SW of Cuatro Ciénegas, *Bacon & Leverich 1144* (TEX), *Bacon & Hartman 1271* (TEX); 14 mi S of Cuatro Ciénegas, then 1.8 mi W, *Turner 6059* (TEX); 15 km SW of Cuatro Ciénegas, *Leverich & Turner 3* (TEX); 38 mi S of Cuatro Ciénegas on Hwy 30, *Bacon & Hartman 1320* (TEX); 68 km SW of Cuatro Ciénegas on hwy to Torreon, *Johnston, Wendt & Chiang 10339* (TEX); 45 mi S of Cuatro Ciénegas on Hwy 30, *Bacon & Dillon 1476* (TEX); 50 mi S of Cuatro Ciénegas on Hwy 30, *Bacon & Hartman 1321* (TEX); 50 mi N of San Pedro de las Colonias on Hwy 30, *Bacon 1025* (TEX); ca. 33 mi N of San Pedro de las Colonias on Hwy 30, *Bacon, Leverich & Turner 1099* (TEX); 42 mi E of Torreon, *Rollins & Tryon 58293* (GH, TEX).

This species shares morphological similarities with *Nerisyrenia johnstonii* (see discussion under that taxon), but on the basis of their flavonoid chemistry and other morphological considerations, the two species are thought to be only distantly related. *Nerisyrenia incana* is closely related to *N. camporum* (see discussion under the latter) as pointed out by Rollins (1939). The latter two species share broad morphological similarities and an almost identical flavonoid chemistry.

This taxon appears to be rather heavily parasitized by certain insects, since plants of this species often have flower buds on the lower 1/3 of the stem arrested in development, with the sepals remaining closed and the structure persisting as a “dried” remnant on its pedicel; or the lowermost fruits of the raceme are often malformed and produce no seeds. Examination revealed the presence of an insect larva in each of these affected parts.



5. **Nerisyrenia camporum** (A. Gray) Greene, *Pittonia* **4**: 225. 1900.

*Greggia camporum* A. Gray, *Smithson. Contrib. Knowl.* **3**(5): 8. 1850. TYPE:

**Texas.** VAL VERDE CO.: *Oct. 1849, Charles Wright 11.* (Holotype, GH!; Isotypes, GH! US!).

*Parrasia camporum* (A. Gray) Greene, *Erythea* **3**: 75. 1895.

Herbaceous perennial, 1–6 dm tall, densely pubescent throughout, the pubescence of short- to long-stalked dendritically branched trichomes, pubescence often canescent-pannose. Stems erect to ascending from an often woody taproot or caudex, branching rather sparsely throughout; older stems to 5 mm thick and often glabrate. Leaves 10–50 mm long, 7–30 mm broad, oblanceolate, obovate, spatulate or, infrequently, elliptic, attenuate to subpetiolate at base, acute to obtuse at apex; margins entire, repand to strongly dentate. Sepals 5–9 mm long, 1–2 mm broad, oblong-oblanceolate in outline, obtuse-subacute at apex; spreading at anthesis, becoming reflexed with age. Petals 8–14 mm long, 5–9 mm broad, obovate, infrequently elliptic; blade margins entire or rarely undulate; dilated and denticulate at base, often the dilation narrow and obscure. Stamens 6.5–9.0 mm long; filaments 4.5–7.5 mm long; anthers 2.0–3.5 mm long. Infructescence 8–35 cm long, lax, usually well exserted above the leaves; pedicels 7–20 mm long, densely pubescent, ascending to divaricately spreading, rarely recurved. Siliques 15–40 mm long, 1.5–4.0 mm broad, linear-oblong to, rarely, somewhat elliptic in outline, strongly obcompressed, straight to strongly curved inward; valves truncate-rounded at apex; pubescence often appearing tufted, the branches of the longer-stalked trichomes ascending; fruit and pedicel, in conjunction, often sigmoid. Style (1.5–)2.0–3.8(–4.3) mm long. Stigma deltoid-sagittate, 0.5–1.5 mm long, somewhat decurrent on the style. Replum 1.0–1.4 mm broad. Seeds 40–100 per silique, 0.8–1.1 mm long, 0.5–0.7 mm broad, elliptic-ovate to oblong; yellow to yellow-brown. Chromosome number:  $2n = 18, 19, 21, 22, 27, 32, 34, 36, 40, 41, 58$ .

**DISTRIBUTION:** Southeastern New Mexico, western and southern Texas, south into Mexico into the states of Chihuahua, Coahuila, Durango and Nuevo León (Figure 5); occurring on gravelly knolls, clay flats, sandy washes and hills, occasionally on gypseous clays in the Big Bend area of Texas and adjacent Mexico. Flowering sporadically throughout the year, primarily February–September.



REPRESENTATIVE SPECIMENS: **México.** CHIHUAHUA: 33 mi N of Jiménez, towards Camargo, *White 2182* (GH, US); 5 mi S of Jiménez, *Johnston 7845* (GH); 1 mi NW of Escalón, *Correll & Johnston 21454* (GH, TEX); ca. 35 mi S of Ahumada, *Bacon & Hartman 1351* (TEX); 8 mi S of Ahumada, *Shreve 9037* (GH); 8 mi W of Hwy 45 along Chihuahua Hwy 2 towards Nuevo Casas Grandes, ca. 12 mi SW of Cd Juárez, *Henrickson 5668* (TEX); ca. 32 mi S of Cd Juárez, 1½ mi E of Samalayuca, *Henrickson 5765* (TEX); Colonia Diaz, *Nelson 6442* (GH, US); ca. 24 mi NE of Julimes, ca. 5 mi S of Rancho El Recuerdo, *Henrickson 13024* (TEX); 8 km N of Progreso, *Stewart 2336* (GH); 5 mi SE from San Carlos, *Johnston & Muller 86* (GH, TEX); 10 mi E of Chapo, *Johnston & Muller 16* (GH, TEX); ca. 28°35'15" N-105°34'17" W at San Diego Hot Springs on Rio Chuisca, *Hewitt 101* (GH); 18.5 mi E of Hwy 16, *Powell, Turner & McGill 2041* (TEX); 23.1 mi SW of Coyame at El Pastor, *Henrickson 6744* (TEX); intersection of Hwy 16 and road to Placer de Guadalupe, *Powell, Turner & McGill 2061* (TEX); 7.5 mi S of Ojinaga, *Powell et al. 2085* (TEX).

COAHUILA: near Rancho Santa Teresa, S of Castanos, *Wynd & Mueller 180* (GH, US); Ojo Caliente, ca. 50 km SW of Monterrey, *Johnson & Barkley 16274m* (GH, TEX); 10 mi E of Saltillo on route 60, *Correll & Johnston 21398* (GH, TEX); 20 mi S of Monclova, *Rinehart 247* (GH); vicinity of Saltillo, *Palmer 324* (GH, US); 33 mi W of Saltillo on Hwy 40, *Bacon 1019* (TEX); 4 mi SW of Hipólito, *Muller 3020* (GH, TEX); 12 mi N of Hipólito, on road to Monclova, *White 1688* (GH); 62 mi W of Saltillo on Hwy 40, *Bacon & Hartman 1344* (TEX); 72 mi E of Torreon, *Rollins & Tryon 58301* (GH); 94 mi W of Saltillo on Hwy 40, *Bacon & Hartman 1345* (TEX); 44 mi E of Torreón, *Rollins & Tryon 58298* (GH, TEX); Puerto Ventanillas, *Stewart 2970* (GH); 12 km E of Tanque Toribio, *Stewart 2981* (GH); 2-3 mi N of San Antonio (ca. lat 27°30'N), *Johnston 8232* (GH, TEX); Paila, *Hinton 16552* (US); Viesca, *Purpus 496* (US); San Lorenzo de Laguna, *Palmer 27* (GH, US); Hermanas, *Marsh 1622* (GH, TEX); 12 mi N of Sabinas Hidalgo, *Heard & Barkley 14541* (TEX); 16 mi N of Nueva Rosita on Hwy 57, *Mahler & Thieret 5645* (SMU); Santa Anna Canyon, near Músqiz, *Marsh 464* (GH, TEX); ca. 120 mi N of Ocampo, *Bacon & Hartman 1291* (TEX); 52 mi N of Ocampo, *Bacon & Hartman 1280* (TEX); 3.7 mi N of Ocampo, *Bacon & Hartman 1272* (TEX); 9 mi E of Cuatro Ciénegas, *Johnston 7104* (GH); "Monte de San Vicente", western base of the Sierra de San Vicente, ca. 20 km ESE of Cuatro Ciénegas, *Schroeder 68* (GH); Cuatro Ciénegas, *Marsh 2064* (GH, SMU, TEX); ca. 35 mi SSW of Cuatro Ciénegas, Sierra de los Alamitos, *Henrickson 13663* (TEX); 4 km W of San Juan, *Stewart 809* (GH); 10 mi E of Los Americanos, 11.5 mi W of La Víbora along Esmeralda-Cuatro Ciénegas RR, *Henrickson 7852* (TEX); 78 mi W of Cuatro Ciénegas, *Bacon & Leverich 1172* (TEX); 115 mi W of Cuatro Ciénegas, *Bacon & Leverich 1188* (TEX); southern end of Laguna de Jaco, *Johnston & Muller 1093* (GH, TEX); La Noria, between Laguna de la Leche and Magueyal, *Johnston 8633A* (GH); Llano de Guaje, 7 mi NE of Penquitas, *Johnston & Muller 350* (GH, TEX); Llano de Guaje, 15 mi E of La India, *Stewart 1182* (GH); 5 km E of Guimbalete, *Stewart 2644* (GH); 8 km E of San José, *Stewart 2647* (GH); base of mtns along the eastern margin of the Valle de Acatita, Rancho Parritas, *Stewart 2775* (GH); Portrero del Cuervo Chico, ca. 3 mi S of Tanque La Ley, *Johnston 8574* (GH); E side of Picacho San José, *Johnston 9406* (GH); vicinity of Santa Elena mines, *Stewart 1929* (GH); 8 km S of Progreso, *Stewart 2299* (GH); vicinity of Castellón, *Stewart 391* (GH); arid plain near Boquillas, *Shreve 8448* (US); Mariscal Canyon of Rio Grande, 11 km downstream from entrance, *Johnston*



12381 (TEX); 6 km E of Mesillas toward Santa Cruz, *Johnston, Wendt & Chiang 11624* (TEX); 5 mi N of Matamoros, *Correll & Johnston 21417* (TEX); 8 mi NW of La Rosa, route 60, *Correll & Johnston 21406* (GH, TEX).

DURANGO: 37.5 mi SW of Gomez Palacios on Hwy 40, *Bacon & Hartman 1323* (TEX); 54 mi SW of Torreon, NE of Cuencame, *Rollins & Tryon 58288* (TEX); 20 km NW of Cuencame, *McVaugh 23630* (GH); 7 mi SE of Conejos, *Correll & Johnston 21439* (GH, TEX); 2 mi W of Bermejillo, *Johnston 7753* (GH); 2 mi NW of Bermejillo on rt 49, *Stuessy 933* (TEX); 14 mi W of Mapimi at Cadena Pass, *Johnston 7758* (GH, US); desert just SW of Pedriceña on Hwy 40, *Mick & Roe 38* (GH).

NUEVO LEÓN: ca. 38 mi SW of Nuevo Laredo, *Webster et al. 11169* (GH); 50 mi S of Nuevo Laredo, *Rivas, Ostos & McCart 8139* (SMU, TEX); 32 mi NNE of Sabinas Hidalgo on 85, *Powell & Turner 2346* (TEX); 17 mi NW of Sabinas on Hwy 85, *Rodriguez 67* (SMU); 12 mi N of Sabinas Hidalgo, *Heard & Barkley 14541* (TEX); 34 mi N of Monterrey on road to Nuevo Laredo, *Frye & Frye 2462* (GH); Monterrey, *Palmer 47* (GH, US); 5 mi N of Espinoza, WNW of Monterrey, *Powell & Turner 2318* (TEX); 5 mi SW of Hidalgo at Parque de Portrero, *Turner & Crutchfield 6266* (TEX).

TAMAULIPAS: 65 km S of Nuevo Laredo, Monterrey hwy, *Dominguez & McCart 8344* (SMU, TEX).

ZACATECAS: northern Zacatecas, *Lloyd & Kirkwood 121* (GH); Cedros, *Lloyd 53* (US); near and at Sierra del Yeso, almost due west of La Presa de Los Ángeles, *Johnston, Wendt & Chiang 11528A* (TEX); 7 km NW of San Juan de Ulúa (Primero de Mayo), *Johnston, Wendt & Chiang 10432C* (TEX).

**United States.** NEW MEXICO: w/o locality, *Wright 1316* (GH); w/o locality, *Wright 1312* (US); plains NE of Parkers Well, 18 Jun 1899, *Wooton s. n.* (US); Doña Ana Co.: foot of Little Mtn, 1 May 1900, *Cockerell s. n.* (US); on and near Tortugas Mtn, *Standley 6434* (US); Tortugas Mtn, SE of Las Cruces, 25 Jul 1895, *Wooton s. n.* (US); Tortugas Mtn, 1 Sep 1908, *Wooton & Standley s. n.* (US); 27 mi NE of Las Cruces, *Shinners 33101* (SMU). Eddy Co.: Malaga, 4 Sep 1946, *Albers 46277* (TEX). Lincoln Co.: Plains S of Lunas Well, 15 Jul 1895, *Wooton s. n.* (GH, US); White Mtns, *Wooton 176* (GH, US). Otero Co.: 2 mi NE of entrance to White Sands Nat'l Monument, *Waterfall 10580* (SMU, TEX); base of Sacramento Mts, Alamo-gordo, 14 Apr 1902, *Rehn & Viereck s. n.* (GH).

TEXAS: w/o locality, May 1881, *Havard s. n.* (US). Brewster Co.: 4 mi SW Adobe Wall Spring, *Turner, Warnock & Parks 1149* (SMU, GH); Del Norte Mtns., *Tharp 3438* (US); Altuda Point, *Warnock 20901* (GH), *21212* (TEX); ca. 15 mi S of Longfellow, *Powell 2130* (TEX); ca. 4 mi S of Marathon on US 385, *Powell 2125* (TEX); 23 mi S of Marathon, *Goodman & Waterfall 4575* (GH, TEX); Texas state road 2627 to La Linda, 9 mi SE of US 285, *Rollins & Correll 6635* (GH, TEX); Frog tank, Black Gap Wildlife Management Area, *Mahler 6313* (SMU); Big Bend Nat'l Park, *Brenckle & Brenckle 51072* (SMU); Juniper Canyon, Chisos Mtns, *Marsh 269* (GH, TEX); ca. 3 mi S of Persimmon Gap, *McVaugh 7834* (SMU, TEX); Dog Canyon Flats, Big Bend Nat'l Park, *Warnock 47063* (SMU, TEX); ca. 8–10 mi S of Dagger Flat, Big Bend Nat'l Park, *Miller & Miller 1276* (SMU); Oak Creek, Big Bend Nat'l Park, *Rollins & Correll 61810* (GH, TEX); mouth of Terlingua Creek, Big Bend Nat'l Park, *Correll & Johnston 18352* (GH, TEX); Castolon Ranger Station, Big Bend Nat'l Park, *Bacon & Hartman 1437* (TEX); Rio Grande river bottom at mouth of Santa Elena Canyon, *Shinners 8796* (SMU); ca. 1 mi SW of jet of road from Santa Elena Canyon and



cutoff to Terlingua, *Webster* 4395 (SMU); arroyo W of Johnson Ranch, Chisos Mtns, *Marsh* 49 (TEX); desert between Alpine and Terlingua, *Nelson & Nelson* 5024 (GH, TEX); 36 mi S of Alpine, *Rose-Innes & Warnock* 21597 (TEX); 3 mi below Study Butte, *Moore & Steyermark* 3247 (GH, US); 4 mi N of Terlingua, *Warnock* 47016 (SMU, TEX); ca. 17 mi SW of jct 118 and FM 170, *Bacon* 1054 (TEX); between Terlingua and the Rio Grande, *Nelson & Nelson* 5046 (GH); Chinatis region, *Nealley* 476 (US). Culberson Co.: 17 mi N of Daugherty, *Waterfall* 4480 (GH); Van Horn, 6 Jun 1905, *Reverchon s. n.* (SMU); Balch Mtn, 5 mi N of Van Horn, *Waterfall* 4450 (GH), 4448 (GH, TEX); 43 mi N of Van Horn on Hwy 54, *Shinners* 33145 (SMU); 18¾ mi SW of Van Horn, *Cory* 44066 (TEX); 30 mi E of Van Horn, *Waterfall* 4192 (GH); Hurd's Draw, *Janszen* 48 (TEX). Dimmitt Co.: Carrizo Springs, 6 Apr 1930, *Hoglund s. n.* (TEX). Duval Co.: 4 mi N of Realitos on Hwy 359, *Cabrera* 51 (SMU, TEX). El Paso Co.: 8 mi E of Fabens on state Hwy 20, *Bacon & Hartman* 1411 (TEX); W edge of El Paso, *Correll* 22602B (TEX); El Paso, *Rose* 4908 (US), *Jones* 3761 (GH, US); Corralitos-El Paso, *Thurber* 745 (GH); island in Rio Grande near El Paso, *Lemmon* 113 (GH); on trail to Cottonwood Springs, E of Canutillo, W side of Franklin Mtns, *Correll & Johnston* 21786 (GH, TEX); McKelligon Canyon, Franklin Mtns, *Warnock* 7670 (SMU, TEX). Hudspeth Co.: S end of Quitman Mtns, 5½ mi NE of Indian Hot Springs, *Waterfall* 4845 (GH); Hwy 80, 8 mi W of Allamore, *Cory* 52888 (SMU, US); Panther Hill-Fox Hill area of central Malone Mtns, *Waterfall* 5818 (GH); E of Finley, *Waterfall* 5029 (GH); foothills S of Guadalupe Peak, 14 Sep 1916, *Young s. n.* (TEX); 12 mi W of Sierra Blanca, *Waterfall* 4576 (GH); 15 mi E of Sierra, *Turner & Warnock* 330 (SMU, TEX); Ft. Hancock exit on IH 10, *Bacon* 945 (TEX); near Ft. Quitman ruins, *Correll* 13778 (SMU, TEX); Jeff Davis Co.: ca. 7 mi from US 90, along road leading from FM 2017 to Candelaria, *Powell* 2189 (TEX); 11 mi NW of Chispa, *Rose-Innes & Warnock* 487 (GH, TEX); Kent, *Jones* 88074 (US). Jim Hogg Co.: Hebronville, *Moran* 9 (TEX). Jim Wells Co.: Amargosa Ranch, 15 mi NW of Alice, *Castillo* 15 (SMU, TEX). La Salle Co.: Cotulla, *Palmer* 11304 (GH, US); Encinal, *Cavazos* 84 (TEX). Loving Co.: between Wink and Mentone, *Warnock* 10631 (SMU, TEX); 3 mi W of Orla, *Rollins & Correll* 6644 (GH); E shore of Red Bluff Lake, *Powell* 2141 (TEX). Maverick Co.: Carrizo Springs-Eagle Pass, *Hogland* 8838 (US); hills near Eagle Pass, *Pringle* 9038 (GH, US). Pecos Co.: 20 to 35 mi S of Ft. Stockton along Sanderson Hwy, *Warnock* 13358 (TEX); Presidio Co.: ca. 3 mi W of Lajitas on Hwy 170 along Rio Grande, *Mahler* 6233 (SMU); 3 mi W of Lajitas, *Powell* 2191 (TEX); Presidio, 28 Apr 1881, *Harvard s. n.* (US); 8 mi N of Presidio along Hwy 67, *Lundell & Lundell* 14291 (TEX, US); 7.5 mi N of Candelaria, *McVaugh* 7980 (SMU, TEX); 1 mi S of Ruidosa, *Tucker* 2992 (GH); 4 mi SE of Ruidosa, *Muller* 8439 (SMU, TEX); 8 mi N of Ruidosa, *Muller* 8425 (SMU, TEX); S end of Van Horn Mtns near Porvenir, *Waterfall* 4749 (GH); ca. 45 mi from Presidio, off Hwy 67, *Lundell & Lundell* 14267 (TEX); near Shafter, *Garrett* 504 (SMU); Thomas Ranch, 28 mi S of Marfa, *Ingram* 2465 (US); ca. 20 mi S of Marfa along FM 169, *Powell* 2129 (TEX); 11 mi S of Marfa, *Rollins & Correll* 6196 (TEX). Reeves Co.: vicinity of Pecos, *Gillespie* 5251 (GH); 22 mi N of Pecos on Hwy 285, *Nelson & Nelson* 4986 (GH, TEX); route 302, 29 mi N of Pecos, *Correll & Johnston* 19073 (GH). Starr Co.: 5 mi N of Rio Grande City, *Crutchfield* 1151 (TEX); off US 283 E of Rio Grande City, *Lundell & Lundell* 9934 (SMU, TEX, US). Terrell Co.: Morton Canyon, about 25 mi S of Dryden, *McVaugh* 7752 (SMU); ca. 11 mi W of Sanderson on US 90, *Averett* 272 (TEX); 42 mi E of Sanderson on route 90, *Gentry & Barclay* 18452



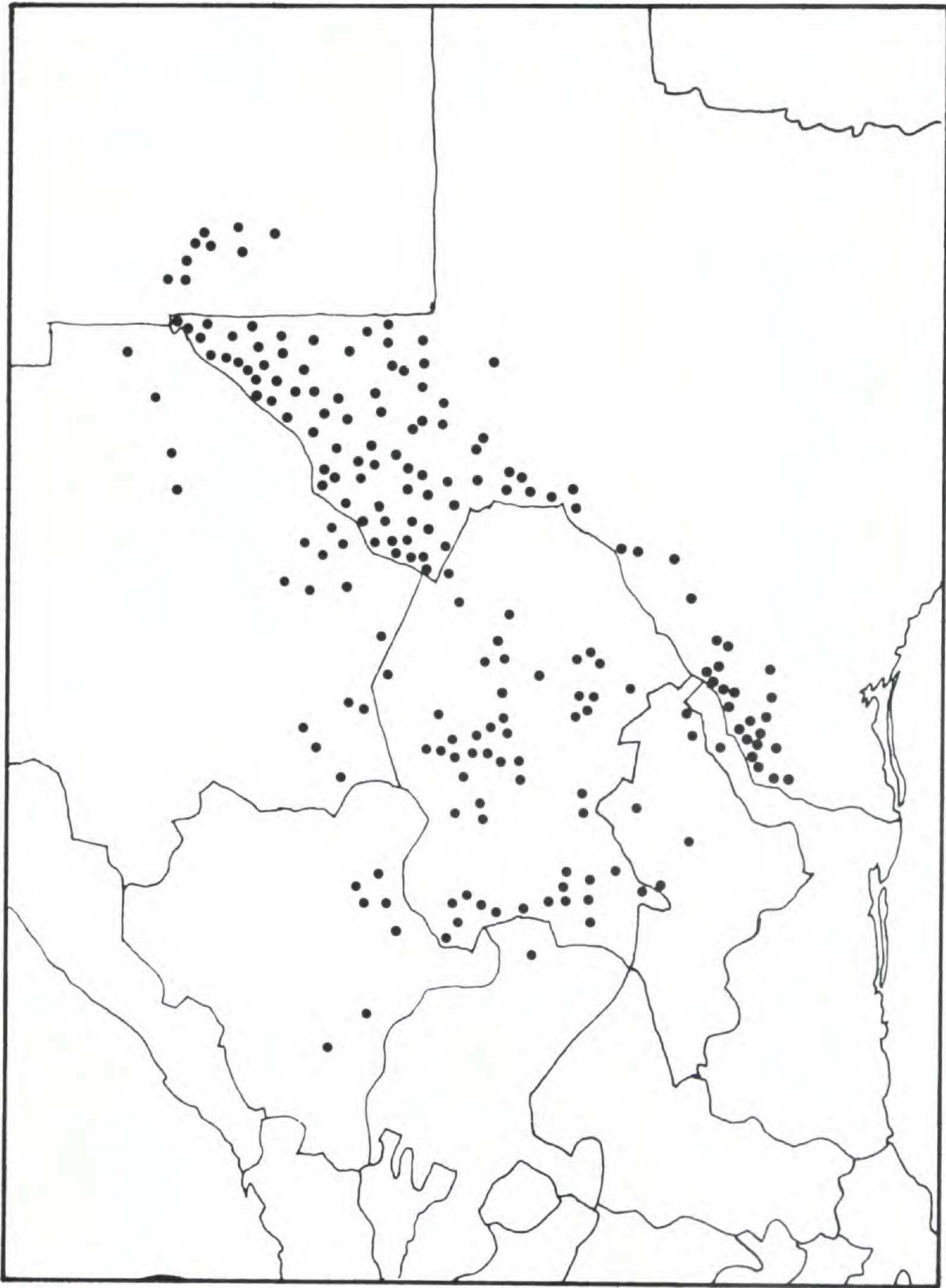


Figure 5. Distribution of *Nerisyrenia camporum*.



(GH, TEX, US); 26 mi W of Langtry, *Wiggins 13362* (US). Val Verde Co.: Soop Road at Del Rio, *Cory 21025* (GH); 3 mi E of Shumla, *Warnock & Cameron 9922* (SMU, TEX); 6 mi E of Langtry, *Rollins & Correll 6157* (GH, TEX). Ward Co.: 5 mi E of Barstow, *Cory 45094* (TEX); Barstow, *Tracy & Earle 25* (GH, TEX, US); 6.4 mi S of Pyote on FM 1927, *Powell 2145* (TEX). Webb Co.: 42 mi N of Laredo, *Rollins & Correll 5943* (GH, TEX); FM 1472, 10 mi N of Laredo, *Paez 125* (SMU, TEX); Lake Casa Blanca, 6 mi NE of Laredo, *Novoa & Cantu 12* (TEX); 10 mi SE of Laredo, *Dickey 123* (TEX). Zapata Co.: S of Laredo, *Rollins 4199* (GH); 13 mi N of San Ignacio, *Shinners 17654* (SMU); Ramireno Ranch, 5 mi S of San Ignacio, *Martinez 31* (TEX); 10 mi N of Zapata, *Cabrera 75* (SMU, TEX); 3 mi S of Zapata on Hwy 83, *Bruno 29* (SMU, TEX). Zavala Co.: Crystal City, 6 Apr 1930, *Hoglund s. n.* (TEX), *Gonzalez 35* (TEX).

*Nerisyrenia camporum* is the most widespread and most variable species in the genus. Plants referred to this species show considerable variation as to plant height, leaf shape and silique length and width. However, I am unable to correlate these morphological expressions with any geographical, cytological or chemical parameters and am, at present, unable to remove any of the variation by taxonomic recognition of regional variants.

This species is closely related to both *Nerisyrenia gypsophila* and *N. incana*. On morphological grounds, *N. camporum* is more like *N. gypsophila*, but chemically it is almost indistinguishable from *N. incana*. These three species are thought to have arisen from a common ancestral plexus, with *N. incana* being an early offshoot from this stock. *Nerisyrenia camporum* and *N. gypsophila* are thought to be later, perhaps contemporaneous, derivatives from this stock, after a dysploid reduction from  $x = 10$  to  $x = 9$  had occurred. Or, *N. gypsophila* may have arisen directly from a peripheral, somewhat aberrant, population of *N. camporum*, through the process of quantum speciation or disruptive selection. Although these species are closely related, they are easily separated and are contrasted below:

<b>N. camporum</b>	<b>N. gypsophila</b>	<b>N. incana</b>
Herbaceous perennials.	Suffruticose.	Suffruticose.
Variously pubescent but never incanous.	Canescent but never incanous.	Incanous.



Leaves not succulent.	Succulent-subsucculent.	Succulent-subsucculent.
Silique apex entire.	Entire.	Notched.
Siliques 1.5–4.0 mm	1.9–3.0 mm broad.	4.0–9.0 mm broad.
Replum 1.0–1.4 mm broad.	0.5–1.1 mm broad.	1.5–3.6 mm broad.

Apparently drawing from the label on the holotype, Rollins (1939) listed the type locality for *Nerisyrenia camporum* as “W. Texas-El Paso, Oct, 1849”. However, Gray (1850, p. 9) in his original description of this species referred to the type locality as “High prairies and calcareous hills, at the head of the San Felipe; July (in flower and fruit).” Presumably, Gray was drawing upon Wright’s original collection data in the citation quoted above.

Gray often united two or more of Wright’s collections, if they represented the same species, and assigned a different number to the united collections (Johnston, 1940). Therefore, it is difficult or impossible to ascertain the original number on which Gray based his description. However, in studying Wright’s original collection data for 1849 (transcribed by Johnston, 1940), and assuming that Gray drew on Wright’s locality citations, two collections appear as likely sources upon which Gray based his description of *Nerisyrenia camporum*. One collection, 610, is listed by Wright as having been collected from “calcareous hills of the San Felipe”; the second, number 636, is listed as “hills, head of S. Felipe”; both collections were made in July. The “San Felipe” referred to in the above quotations is San Felipe Creek or San Felipe Springs, the source for the creek, both of which are located near present day Del Rio in Val Verde County, Texas (Johnston, 1940). The locality data for the two collections cited above is very similar to that given by Gray, suggesting that one (or both) of the above collections represents the type of the species to which Gray assigned the number 11. Although Wright collected in far western Texas during September, October and November of 1849, none of his collections from that region or during that time span bear any reference to a “San Felipe”.



6. **Nerisyrenia gypsophila** Bacon sp. nov. TYPE: **México**. CHIHUAHUA: Jurassic gypsum ca. 15 miles SE of Estación Morreon on Rio Conchos lake road, Sierra de las Monillas. 26 May 1971. *A. M. Powell et al.* 2108. (Holotype, TEX!; Isotypes, to be distributed).

Suffrutices 2.5–3.5 dm alta. Radix palaris crassa. Caules plures vel multi erecti vel adscendentes, ramis praecipue ad partem superiorem restrictis, dense pubescentes saepe canescentes trichomatibus nonnihil adpressis dendriticis brevistipitatis longistipitatisve, vetustiores ad 7 mm crassi cortice exarata aliquantum exfolianti saepe glabrata. Folia 16–40 mm longa (2–)5–8(–11) mm lata, plus minusve succulenta, oblanceolata vel anguste elliptica base attenuato-subpetiolata apice acuta vel subacuta margine integra vel repando-dentata saepe leviter revoluta, dense pubescentia saepe pannosa trichomatibus dendriticis brevistipitatis longistipitatisve. Sepala 6.5–8.5 mm longa 1.1–1.2 mm lata lanceolata vel oblanceolata apice acuta per anthesin effusa demum reflexa dense pubescentia trichomatibus dendriticis sessilibus brevistipitatisve. Petala 9.5–11.5 mm longa 4.5–8.5 mm lata anguste obovata vel elliptica base conspicue dilatata denticulataque. Stamina 5.5–8.5 mm longa, filamenta 4–6 mm longa, antherae 2.4–3.4 mm longae. Infructescentia admodum rigida 4–30 cm longa parte superiore in folia non inclusa parte inferiore saepe inclusa; pedicelli 8–12 mm longi, satis recte adscendentes raro effusi haud divaricati, dense pubescentes trichomatibus dendriticis longistipitatis brevistipitatisve, inferiores paucillum dispersi superiores leniter congesti. Siliquae ad maturitatem imbricatae dense vel leniter congestae, 17–30 mm longae 1.9–3.0 mm late lineari-oblongae valde obcompressae, rectae haud arcuatae; valvae apice rotundatae truncataeve, dense pubescentes trichomatibus saepe flocculosis. Stylus 2.7–4.0 mm longus glaber, vel raro trichomatibus dendriticis paucis. Stigma 0.6–1.0 mm longum sagittatum vel rotundatum raro aliquantum decurrens. Replum 0.5–1.1 mm latum. Semina 0.6–1.0 mm longa 0.5–0.7 mm lata, ovata vel anguste oblonga, turgida vel leviter compressa, ochracea. Chromosomatum numerus:  $2n = 18$ .

DISTRIBUTION: Presently known only from the type locality and immediate vicinity (Figure 3), occupying crusty gypsum exposures and gypseous soil of alluvial fans. Flowering from March to September.



REPRESENTATIVE SPECIMENS: **México.** CHIHUAHUA: 1.2 mi SE of Hwy 16 on road to Rio Conchos Lake, *Powell et al. 2102 & 2103* (TEX); 11.8 mi S of Aldama-Ojinaga Hwy, 27.4 mi N Aldama, *Bacon & Hartman 1348* (TEX); 8.8 mi E of RR, Hwy 16, *Powell, Turner & McGill 2069* (TEX); 11 mi E of Hwy 16 on road to new lake on Rio Conchos, *Powell, Turner & McGill 2026* (TEX); 1.7 mi S of Placer de Guadalupe, *Powell, Turner & McGill 2054* (TEX).

This species is most closely related to *Nerisyrenia camporum*. It is, however, easily distinguished from that taxon by several morphological features (see discussion under *N. camporum*).

The taxon is thought to have arisen through some quantum event or disruptive selection, as its ancestors encountered gypseous localities; its impoverished flavonoid chemistry, as compared to *Nerisyrenia camporum*, might reflect, in part, physiological variation associated with individuals in the ancestral population which were genetically predisposed towards occupation of this unusual soil type.

7. ***Nerisyrenia linearifolia*** (S. Watson) Greene, *Pittonia* **4**: 225. 1900. For synonymy and typification, see varietal designations.

Herbaceous to somewhat woody, rhizomatous perennial, 0.5–4.0 dm tall, moderately to densely pubescent throughout with sessile to long-stalked, dendritically branched hairs; stems few to several from a woody caudex, erect to somewhat spreading, older stems to 5 mm thick. Leaves 16–70 mm long, 1.2–8.0 mm broad, more or less succulent, terete to flattened, overlapping on the stem; linear to narrowly oblanceolate-spathulate, attenuate at base, obtuse to acute at apex; margins entire, weakly sinuate to rarely dentate. Sepals 4.8–7.5 mm long, 1.0–2.0 mm broad, broadly lanceolate, ovate to elliptic in outline. Petals 8.5–13.0 mm long, 5.0–8.5 mm wide, obovate to spathulate in outline; blade margins entire; dilate and denticulate at base. Stamens 6.0–8.5 mm long; filaments 4–6 mm long; anthers 2.5–3.5 mm long. Infructescence 5–35 mm long, lax; pedicels 6–16 mm long, ascending, divergent to divaricate, not congested toward the apex. Siliques 9–30 mm long, 1.0–3.6 mm broad, oblong to weakly obclavate-subulate in outline, terete to usually somewhat obcompressed, straight to incurved; valves somewhat angled to the margin, rounded-truncate at apex, rarely tapered to the style. Style glabrous, 0.9–4.0 mm long. Stigma deltoid-sagittate, 0.4–1.5 mm long, somewhat decurrent on the style. Replum 0.7–1.3 mm broad. Seeds 30–80 per silique, ovate-elliptic to oblong, plump to slightly flattened; yellow.



## KEY TO THE VARIETIES

Plants low and clump forming, branching throughout, siliques widest at base, weakly obclavate-subulate in outline. . . . . 7a. var. *mexicana*.

Plants more erect, branching restricted to upper 2/3 of stems, siliques not widest at base, oblong in outline. . . . . 7b. var. *linearifolia*.

7a. ***Nerisyrenia linearifolia* var. *mexicana*** Bacon var. nov. TYPE: **México.** COAHUILA: Agua Nuevo, 18 Apr 1905, *E. Palmer 560*. (Holotype, GH!; Isotype, US!).

Herbae perennes humiles 1–2 dm altae. Caules decumbentes vel adscendentes omnino ramosi. Folia 19–70 mm longa 1.5–8.0 mm lata complanata anguste oblanceolato-spathulata, basi attenuata apice obtusa vel acuta. Infructescentia 6–19 cm longa. Pedicelli 8–16 mm longi divaricate adscendentes vel effusi vel aliquando recurvati. Siliquae 15–27 mm longae (1.5–)2.3–3.6 mm latae, plerumque basi latissimae, paululum obclavato-subulatae. Replum ad 1 mm latum. Chromosomatum numerus:  $2n = 36$ .

**DISTRIBUTION:** A gypsum endemic, found in loamy to hard-packed clays in the southeastern quarter of Coahuila, southern half of Nuevo León and adjacent areas of Tamaulipas and San Luis Potosí (Figure 6). Flowering from April to December.

**REPRESENTATIVE SPECIMENS:** **México.** COAHUILA: Agua Nuevo, *Palmer 560* (GH); 15 mi S of Saltillo, *Rollins & Tryon 58130* (GH, TEX); 31 mi SW of Monterrey, *Warnock & Barkley 14740m* (TEX); Hipólito, *Viereck 516* (US); S of Paila (Valle Seco), *Hinton 16552* (US); Parras, *Palmer 1047* (GH, US). NUEVO LEÓN: 4.5 mi N of Matehuala, *Beaman 1860* (GH, US); 4.5 mi E of San Roberto Jet on Hwy 60, *Bacon & Hartman 1337* (TEX); 5.3 mi E of San Roberto, *Bacon 1008* (TEX); 11.5 mi E of San Roberto Jet on road to Linares, *Turner & Crutchfield 6315* (TEX); 29 mi W of Galeana, *Rollins & Tryon 58175* (GH); on a flat W of Galeana, *Rinehart 328* (GH); near Pablillo, *Shreve & Tinkham 9748* (GH); 21 mi E of Saltillo, *Rollins & Tryon 58105* (GH, TEX). SAN LUIS POTOSÍ: 18 km S of San Luis Potosí, *Rollins & Tryon 58211* (GH, TEX); 15 mi E of La Presa, *Barkley, Rowell & Paxson 844* (TEX); along road between Dr. Arroyo and Matehuala, *Nelson 4526* (GH, US). TAMAULIPAS: Reservoir of Miquihuana, *Stanford, Lauber & Taylor 2372* (US); Miquihuana, *Viereck 541* (US).

*Nerisyrenia linearifolia* var. *mexicana*, on further study, may prove to be worthy of specific status. I have had little field experience with the variety, and consequently, my knowledge of the taxon is derived primarily from herbarium specimens. In overall morphological expressions, it appears quite distinctive. However, it is



difficult to find specific characteristics, singly or in combination, which readily distinguish the two varieties. Until I have a better acquaintance with this taxon, I have opted for a conservative view and treat the entity as only varietally distinct.

7b. **Nerisyrenia linearifolia** (S. Watson) Greene var. **linearifolia**.

*Greggia linearifolia* S. Watson, Proc. Am. Acad. **18**: 191. 1883. TYPE here designated: **Texas**. CULBERSON CO.: bluffs of Delaware Creek, 1882, *V. Havard s. n.*, right-hand members on sheet. (Holotype, GH!).

*Greggia camporum* Gray var. *angustifolia* Coulter, Contr. U. S. Nat. Herb. **1**: 31. 1890. TYPE: **Texas**. IRION CO.: Camp Charolette, *Nealley 702*. (Holotype, US!).

*Greggia camporum* Gray var. *linearifolia* (S. Watson) M. E. Jones, Proc. Calif. Acad. **5**: 625. 1895.

*Parrasia linearifolia* (S. Watson) Greene, Erythea **3**: 75. 1895.

Herbaceous to somewhat woody, rhizomatous perennial, 1.5–4.0 dm tall; stems ascending-erect, rarely spreading; branching confined to upper 2/3 of stem. Leaves 16–65 mm long, 1.2–4.5 mm broad, terete to flattened; linear to narrowly oblanceolate-spathulate, attenuate at base, acute to obtuse at apex. Infructescence 5–35 cm long; pedicels 6–14 mm long, ascending to divergent. Siliques 9–30 mm long, 1.0–2.2 mm broad, oblong in outline. Replum 0.7–1.3 mm broad. Chromosome number:  $2n = 18, 19, 20, 34, 36$ .

**DISTRIBUTION:** Southeastern New Mexico and west Texas; a single outlying population known in the Sierra de la Paila, Coahuila (Figure 6); an edaphic endemic restricted to gypsum outcrops or heavily gypseous sandy or loamy-clay soils. Flowering sporadically throughout the year, primarily February to September.

**REPRESENTATIVE SPECIMENS:** **México**. COAHUILA: Mina la Abundancia in upper reaches of Cañón Corazón del Toro, SW quadrant of Sierra de la Paila, *Chiang, Wendt & Johnston 10118* (TEX); Sierra de la Paila, SW quadrant, *Wendt, Chiang & Johnston 10111A* (TEX); Sierra de la Paila at one of the lower mine levels in the Mina la Abundancia area, *Johnston, Wendt & Chiang 10510* (TEX).

**United States.** NEW MEXICO: Chaves Co.: ½ mi SW of Fraier, *Waterfall 6132* (GH, SMU); 20 mi NE of Roswell, *Goodman & Hitchcock 1133* (GH); Ft. Sumner-Roswell, *Nelson 11311* (GH); E embankment of Pecos River by Roswell, Hwy 380, *Solbrig 3177* (GH). Doña Ana Co.: White Sands, *Wooton 158* (US). Eddy Co.: 16.5 mi SE of Carlsbad on Hwy 128, *Bacon & Hartman 1397* (TEX); Lakewood, 6 Aug 1909, *Wooton s. n.* (US). Lincoln Co.: 35 mi S of Torraine, 10 Aug 1909, *Wooton s. n.* (US). Otero Co.: 32.1 mi NE of Las Cruces, *Bacon 1046* (TEX); 18 mi SW of entrance to White Sands Nat'l Monument, *Turner & Turner 8017* (TEX); White Sands, *Berkman, Lee & Tharp 46060* (SMU, TEX). Socorro Co.: 21 mi W of



Carrizozo on Hwy 380, *Bacon & Hartman 1389* (TEX). TEXAS: Crane Co.: off US 67, 6 mi W of McCamey, *Lundell & Lundell 10220* (SMU, TEX, US); 6.5 mi W of McCamey on Hwy 67, *Bacon 1468* (TEX); 5–8 mi N of Imperial, *Warnock 15438* (TEX); ca. 10 mi E of Grandfalls, *Hinckley & Hinckley 208* (SMU, US). Culberson Co.: 31 mi NW of Kent, *Muller 8492* (SMU); 33 mi W of Orla on Hwy 652, *Bacon & Hartman 1406* (TEX); 6 mi E of Delaware Springs, *Correll & Johnston 18538* (GH, TEX); ca. 15 mi E of Pasotex pipeline headquarters on Delaware Creek, Pasotex pipeline road, *Rollins & Correll 61147* (GH, TEX); 22 mi SE of State Line Cafe, Texas RR 652, *Rollins & Correll 6642*, in part, (GH); 1 mi S of Texas-New Mexico line on Hwy 62, *Waterfall 3749* (GH); 30 mi N of Van Horn, *Waterfall 4129* (GH); 44 mi N of Van Horn, on Hwy 84, *Correll & Johnston 18468* (GH, TEX); 1.5 mi E of Daugherty, *Waterfall 5183* (GH); 5 mi N of Daugherty, *Waterfall 4471* (GH); 22 mi SE of State Line Cafe, Texas RR 652, *Rollins & Correll 6643* (GH, TEX); 1.7 mi S of NM State line, Texas RR 1108, *Rollins & Correll 6640* (TEX); 2 mi SE of US routes 62 & 180 at New Mexico line, *McVaugh 8162* (GH, SMU, TEX). Hudspeth Co.: W side of Salt Lake on Hwy 62, *Whitehouse 17001* (SMU); SE base of Malone Mts, *Correll & Johnston 19295* (TEX). Pecos Co.: along Pecos River Girvin, *Warnock 208* (US). Reeves Co.: 5 mi E of Pecos, Toyah Lake, *Warnock 5252* (SMU, TEX); 6 mi E of jct FM 1450 & 285, on 1450, *Bacon & Hartman 1360* (TEX); 12 mi NW of Toyah, *Tharp & Gimbrede 51-997* (TEX); 7 mi SE of Pecos, *Turner 931* (SMU); 4 mi N of Pecos, *Waterfall 4226* (GH); 56 mi N of Pecos, *Waterfall 4255* (GH); 12 mi W of Mentone on Hwy 285, *Bacon & Hartman 1405* (TEX). Ward Co.: 12 mi S of Monahans, *Turner & Warnock 59* (GH); 5 mi E of Barstow, *Cory 45096* (TEX); 6.4 mi S of Pyote, near FM 1927, *Powell 2146* (TEX); 2 mi W of Pyote, *Warnock 7872* (SMU, TEX). Winkler Co.: 10 mi S of Kermit on State Hwy 18, 1 mi W on county road, *Collins 1304* (SMU); 12 mi SSE of Kermit, *Rowell 11540* (SMU).

This variety often occurs in marginal sympatry with *Nerisyrenia camporum*. The two species are ecologically isolated, however, since *N. camporum* is, for the most part, calciphilic instead of gypsophilic. Morphologically, these two species are easily separable since the one species is rhizomatous with relatively narrow leaves, while *N. camporum* is taprooted with much broader leaves.

This taxon is restricted, for the most part, to western Texas and southeastern New Mexico. Nevertheless, I refer here, albeit with hesitation, three collections from the Sierra de Paila in southern Coahuila. These collections exhibit the upright, more robust habit, with narrow linear leaves typical of *Nerisyrenia linearifolia* var. *linearifolia*. The fruits of these plants (available only on one collection, *Johnston, Wendt & Chiang 10510*) are much reduced in length and more strongly obcompressed than is typically found in this variety. These collections may represent another as yet undescribed species of *Nerisyrenia*; however, until more field observations and further study of plants from the above area can be made, I accept them as relatively atypical members of this taxon.



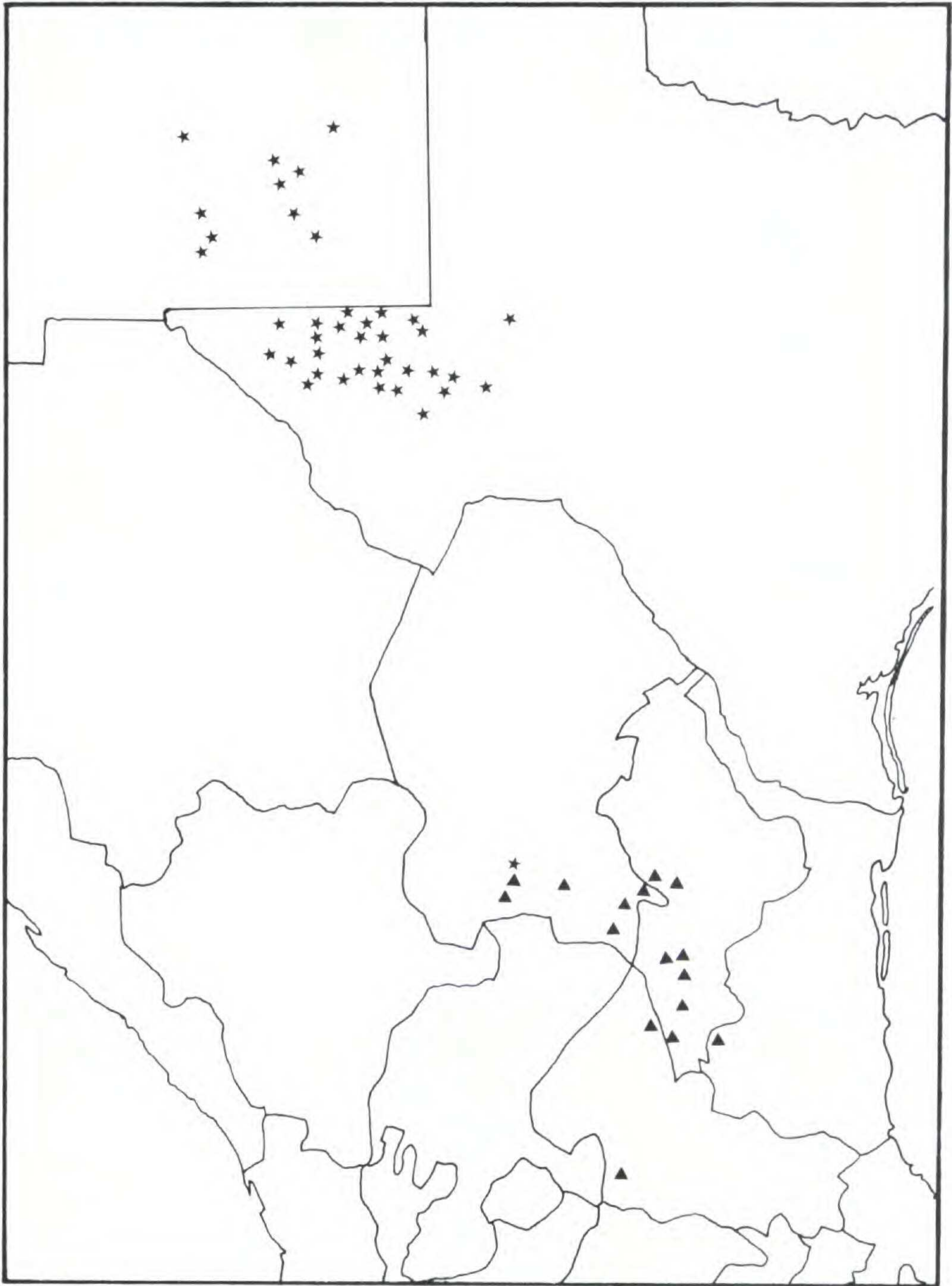


Figure 6. Distribution of *Nerisyrenia linearifolia*: var. *linearifolia*, closed stars; var. *mexicana*, closed triangles.



8. **Nerisyrenia gracilis** I. M. Johnston, Jour. Arnold Arb. **22**: 157. 1941. TYPE: **México**. SAN LUIS POTOSÍ: gypsum plains near sinkholes; stems decumbent; corolla white; 2 miles south of Cedral, 11–12 Sep 1938, *I. M. Johnston 7583*. (Holotype, GH!).

Herbaceous to somewhat woody, rhizomatous perennials, 0.5–1.5 (rarely to 4) dm tall, scattered to densely pubescent throughout with sessile or short-stalked dendritically branched trichomes; stems several from a slender, woody caudex, usually decumbent, occasionally ascending; older stems to 3 mm thick, often with furrowed bark, glabrate. Leaves succulent, 20–70 mm long, 0.7–2.5(–6) mm broad linear-oblong to spatulate, terete to flattened, attenuate at base, obtuse to acute at apex; margins entire, rarely with 1 or 2 dentations. Sepals 3.5–6.5 mm long, 0.7–1.5 mm broad, lanceolate, subulate, rarely oblong in outline, acute-obtuse at apex. Petals 7–10 mm long, 3.5–6.0 mm broad, obovate-spatulate in outline, obtuse at apex, margins entire to somewhat undulate; dilated and denticulate at base. Stamens 5–8 mm long; filaments 4–6 mm long; anthers 2.0–3.5 mm long. Infructescence rather lax, (2.0–)4–17(–20) cm long, often the apical fruits barely exceeding the leaves, basal fruits included within the leaves; pedicels 5–9 mm long, ascending to spreading, rather evenly spaced throughout. Siliques slender, 6–30(–35) mm long, 0.7–1.3(–2.0) mm broad, terete, rarely compressed, straight to curved inward to tortuous; valves commonly somewhat thin and outlining the seeds, tapering to the style. Style 1.8–3.8 mm long, glabrous. Stigma 0.5–1.1 mm long, deltoid-sagittate, decurrent on the style. Replum 0.9–1.2(–1.6) mm broad. Seeds 30–90 per silique, 0.5–0.7 mm long, 0.5–0.6 mm broad, broadly ovate to oblong, plump; yellow. Chromosome number:  $2n = 18, 34, 36, 38$ .

**DISTRIBUTION:** Southwestern Nuevo León, southeastern corner of Coahuila, eastern Zacatecas and northeastern San Luis Potosí, Mexico, occupying crusty to hard-packed or exposed gypsum plains and flats (Figure 3). Flowering from March to September.

**REPRESENTATIVE SPECIMENS:** **México**. COAHUILA: Hipólito, *Viereck 516* (US); 6 mi N of La Ventura, *Johnston 7638* (GH). NUEVO LEÓN: Minas “Manto Blanco” y “Sabana Blanco”, just N of the Cañón de Portrerillas, *Johnston, Wendt & Chiang 10251a* (TEX); 16 mi N of Rancho de Estacas, on the road to Rancho Lechuguillal, *Johnston, Wendt & Chiang 10214* (TEX); Km 100 on Hwy between Monterrey and Monclova, *Bacon, Leverich & Turner 1077 & 1079* (TEX); 105 km on Monterrey-



Monclova Hwy, *Bacon, Leverich & Turner 1081 & 1082* (TEX); 29.5 mi SE of jct Mex 53-57, near Mex 53, *Powell & Turner 2297* (TEX); 100 km NW of Monterrey, *Turner 6365* (TEX); ca. 10 mi S of San Jose de Raices on Mex 57, *McVaugh 18230* (GH); ca. 28 mi N of San Roberto on Hwy 57, *Bacon, Leverich & Turner 1104* (TEX); 7.3 mi N of San Roberto Hwy 57, *Bacon 1013* (TEX); Km 154 on Hwy 57, *Bacon, Leverich & Turner 1108 & 1109* (TEX); 8 mi S of Galeana, *Correll & Johnston 19870* (TEX); 4 mi S of Galeana, *McGregor et al. 71* (GH); 2.5 mi S of Pueblo Galeana, *Irving 152* (TEX), *Stuessy 268* (TEX); 15 mi S of San Roberto, *Turner 6215* (TEX); 15 mi S of San Roberto Jct on Mex 57, *Sanderson 293* (TEX); 17 mi S of San Roberto on Hwy 57, *Bacon, Leverich & Turner 1119* (TEX); 66 km S of San Roberto jct on road to San Luis Potosí, *Chiang, Wendt & Johnston 8258B* (TEX); 40 mi N of Matehuala, *Waterfall 15756* (SMU). SAN LUIS POTOSÍ: 6 mi N of San Vicente, *Johnston 7616* (GH); 13 mi N of Matehuala, *Shreve 8709* (US); 3.5 mi N of Matehuala, *Bacon & Hartman 1335* (TEX); 3-5 mi N of Matehuala, towards Cedral, *Henrickson 6551* (TEX); just W of Hwy 57 on road to Cedral, *Bacon Leverich & Turner 1127* (TEX); 4.3 mi W of Hwy 57, on hwy to Cedral, *Bacon 1001* (TEX); 7.5 mi W of Hwy 57, on road to Cedral, *Bacon 1002* (TEX); 1.7 mi S of Cedral, *Bacon 1004* (TEX); 5 mi S of Cedral, *Johnston 7525* (GH); 38 mi S of Matehuala, *Johnston 7509* (GH); gravelly plain E of Catorce, *Pennell 17554* (TEX). ZACATECAS: Vanegas-Salttillo road, *Lundell 5725* (TEX, US); 35 mi NNW of Concepción del Oro, 10 mi W of Cedros, *Henrickson 6349* (TEX); Cedros, *Lloyd 111* (US); Sierra Hermosa, *Johnston 7402* (GH, US).

Johnston (1941) suggested that this species was most closely related to *Nerisyrenia linearifolia* (var. *linearifolia* of this treatment). However, due to the distinctive differences in flavonoid chemistry and, also, to morphological differences between this species and *N. linearifolia*, I consider *N. gracilis* to be most closely related to *N. powellii*.

9. ***Nerisyrenia powellii*** Bacon sp. nov. TYPE: **México**. COAHUILA: gypsum outcrops between El Rey and Laguna del Rey on road from El Rey to La Chemica, 19 Oct. 1971, *J. D. Bacon & W. R. Leverich 1257*. (Holotype, TEX!; Isotypes, to be distributed).

Suffrutex rhizomatosus 2-4 dm altus; caules plures erecti vel aliquantum effusi copiose ramosi, vetustiores ad 0.7 cm crassi glabrescentes cortice exarata. Folia succulenta 15-40 mm longa 2-5 mm lata lineari-spathulata basi attenuata apice obtusa vel acuta margine integra vel raro 1-2 dentibus. Sepala 5-7 mm longa 1-1.5 mm lata, subulata vel oblanceolata, apice acuta, patentia demum reflexa, dense pubescentia trichomatibus dendriticis brevistipitatis vel longistipitatis. Petala 6-9 mm longa 3-5 mm lata, spathulata vel anguste obovata basi dilatata. Stamina 5-8 mm longa, filamenta 4-6 longa, antherae 3-4 mm longae. Infructescentia laxa



15–23 cm alta plerumque multo elevata super folia; pedicelli 5–10 mm longi adscendentes raro recurvati, dense pubescentes trichomatibus dendriticis brevistipitatis longistipitatisque. Siliquae 9–25 mm longae 1–1.5 mm latae teretes vel saepius parum compressae, rectae vel parum introrsum arcuatae; valvae versus stylum angustatae, apice acutae vel subacutae saepe ad maturitatem tenuiores et leniter constrictae inter semina. Stylus 2.3–2.8 mm longus. Stigma 0.6–0.9 mm altum, plus minusve decurrens in stylo. Replum 1–2 mm latum elliptico-oblongum apice saepe acutum. Semina 30–80 ovato-oblonga turgida flava. Chromosomatum numerus:  $2n = 38$ .

**DISTRIBUTION:** Plants endemic to northern Coahuila, occupying chalky gypsum outcrops, crusty gypsum knolls and gypseous clay flats of valley floors (Figure 3). Flowering from March to October.

**REPRESENTATIVE SPECIMENS:** **México.** COAHUILA: between la Víbora and Matrimonio Viejo, about lat. 27°6'N, *I. M. Johnston* 9336 (GH); 4½ km E of Matrimonio Viejo, *M. C. Johnston, Wendt & Chiang* 10898 (TEX); 76.3 mi W of Cuatro Ciénegas, *Bacon & Leverich* 1159 (TEX); 3 mi from San Vicente, *Stewart & Johnston* 1953 (GH, TEX); along road from San Vicente to southern end of Laguna de Jaco, *Johnston & Muller* 1078 (GH, TEX); *Johnston & Muller* 1099 (GH, TEX); 16 mi S of Laguna del Rey, *I. M. Johnston* 7814 (GH); E side of Picacho San José, S of Santa Elena, *I. M. Johnston* 9406 (GH).

*Nerisyrenia powellii* is most closely allied to *N. gracilis*. The two species are allopatric, however, and cannot be confused since *N. powellii* is an erect, suffruticose perennial while *N. gracilis* is a decumbent, herbaceous perennial. (See discussion under *N. castil-lonii*).

This species is known from only a few collections and may yet be found over a larger region. However, in at least some areas it forms large, rather uniform populations such as those which I have seen occupying extensive gypsum exposures on the northwest side of Laguna del Rey.

The species is named for Dr. A. M. Powell, whose teachings and personal attitudes greatly influenced my appreciation of botany.

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